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The Origin of Sexuality	***E. C. Dougherty***	**145**
Pogonophora	***A. V. Ivanov***	**170**
Microgeographic Races in Mammals	***J. K. Doutt***	**179**
In Defense of the Subspecies	***S. D. Durrant***	**186**
Points of View	***Zalokar; Parkes***	**191**

Index for Volume 4 (1955)

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Systematic Zoology

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Comparative Evolution and the Origin of Sexuality

ELLSWORTH C. DOUGHERTY

IN COMPARATIVE evolution, or, more exactly expressed, the study of evolution[1] from the comparative viewpoint, one is concerned with evolutionary patterns in different phylogenetic lineages or in a given lineage at different periods in time, or both. Thinking in such terms involves certain difficulties not generally encountered in most other disciplines of comparative biology, for in the former case it is not some contemporary morphological or physiological system in two or more groups of organisms, or some ecological system in two or more situations that is being compared, but two or more reconstructions, or parts of a single reconstruction, based largely on extrapolation of present-day attributes backward in time, though aided, it is true, to varying degrees by geological data—in some cases especially by the fossil record, through which certain ancestral attributes can be directly observed. In other words, in comparative metatropology, one deals to an important extent with theoretical concepts, as opposed to observable facts, about mechanisms. This means that it cannot be an exact discipline in the sense of comparative morphology and physiology. Nevertheless, it is capable of illuminating important biological problems, even of providing or suggesting answers that are not otherwise accessible.

It is an obvious, yet often overlooked fact that all contemporary living forms have a long concomitant evolution. It even follows from the theory of a common ancestry of all cellular organisms, to which I subscribe, that they are equally ancient. This means that entities as disparate as the bacteria and the most complicated metazoans are of the same antiquity—not, of course, in their present form, but in their phylogenetic history. The coexistence, at any time, of organisms of varied levels of morphological complexity—hence of increasing degrees of departure from the primitive common ancestor (usually, though not always, correlated with increased complexity)—is one of the most interesting aspects of comparative metatropology. It is to be explained by the fact that metatropic (evolutionary) diversification has proceeded by a branching process and that some of the branches have evolved at greatly different rates.

One very important type of problem, which for solution must be subjected to the disciplined thinking essential to comparative metatropology, is whether or not a given feature, common to contemporary representatives of two or more phylogenetic lineages, constitutes an evolutionary heritage from a common ancestor, or a convergent property independently achieved in each case (or at least in some of the cases).

[1] A single word is needed to replace the awkward expression, "study of [organic] evolution." The exact Greek equivalent of the Latin *evolutio (an unfolding)* is ἀνάπτυξις [anaptyxis], but this does not provide a stem for a euphonious abstract word and, moreover, has been preëmpted in English as a term in phonetics. A simple neologism for evolution based on Greek could be *metatropy* (from μετά—*thereafter, beyond;* and τρόπος—a *turning*: hence, *a turning* or *changing beyond,* or, by extension, *evolution*). From this one may derive the word *metatropology* (from metatropy + λόγος — *a word, discourse*)—the study of evolution. I am indebted to Professor Frederic Peachy, Department of Classics, University of California, Berkeley, for this analysis. Where needed, the word metatropology and its cognates and derivatives are used henceforth in this paper.

I propose in this paper to treat the origin of *sexuality* as a problem in comparative metatropology. I wish to make clear at once what I mean by "sexuality" and "sexual mechanisms." The definition of "sex" has been diverse—as is well illustrated in the varied usages to be found in the recent A.A.A.S. monograph, *Sex in Microorganisms* (see Wenrich, 1954*b*). I use the word *sexuality* to mean that property of organisms displayed *when they regularly establish new combinations of self-duplicating, desoxyribosenucleic acid (DNA)*[2] *molecules, or aggregates thereof, either by merging of two separate cellular compartments or by the transfer of such material otherwise from one cellular compartment to another, usually of the same species,* where such molecules are part of the usual hereditary material of the cells involved and where the transfer is not simply that transmission of hereditary material occurring when a cellular compartment duplicates itself by vegetative means; the word *sexuality* thus also comprehends *those processes, made necessary by transfer mechanisms, that permit the sorting out and/or recombination of such molecules (in part, in whole, or in groups) within a cell.* The latter processes may be separated from the former by many vegetative cellular reproductions in some living entities. One may therefore usefully distinguish mechanisms of *transfer* and *recombination* respectively.

I mean to include as categories of sexuality various patterns of parthenogenesis even though they do not strictly involve the transfer of DNA between cellular compartments, and even though some of them do not even result in recombination of DNA within the cell. I agree with Boyden (1953) in holding this point of view—namely (as I should express it), that parthenogenetic mechanisms are specializations of sexual mechanisms, involving formation of gametes (or of some comparable, specialized cell or group of cells), wherein transfer mechanisms and sometimes recombination mechanisms are secondarily lost.

I do not, however, mean to include as categories of sexuality the transmission, between cells, of symbiotic microörganisms—whether parasitic, commensalistic, or mutualistic—if the phylogeny of the latter has been long independent of the host cells. It seems logical to hold that, where such transfer exclusively involves infection with an organism of separate phylogenetic history, the process in question should not be considered sexual. But one runs into difficulties with the viruses. In bacteria, for example, certain processes, which are clearly sexual in the sense advocated here, are tied up with viral transfer, and it is not in fact possible to distinguish clearly between sexuality and infection in these cases. This problem is treated later in the present paper.

The paramount question arising out of a consideration of the origin and significance of sexuality as a problem in comparative metatropology, has been recently formulated by Wenrich (1954*b*, p. 341), who has, however, made no direct effort to answer it. It may be expressed in alternative terms: (1) can sexuality be regarded as a very early and primitive property of living systems, possibly of a

[2] The significance of ribosenucleic acid (RNA) in connection with the problems discussed in the following pages is still obscure. Its structure is still poorly known (Rich and Watson, 1954), and, moreover, it does not appear to have anything comparable to the central importance of DNA in modern heredity. On the other hand, my essentially exclusive preoccupation with DNA may ultimately be unmasked as a gross oversimplification. It has proved a relatively simple substance (or class of substances) to isolate and even to characterize structurally (Feughelman *et al.*, 1955) and thus may be assuming a position of prime importance in current biological thinking that in actual fact it should share with other substances. We must be ever on the alert to recognize even more fundamental, though less easily demonstrable, phenomena in which genetic continuity is under the control of such other substances (as, for example, proteins, either linked up directly or not with nucleic acid). Having made this point, I nevertheless am presenting in this paper, as the reader will easily recognize, a set of theories essentially oriented about DNA as the supreme arbiter of heredity.

single origin in the evolution of life; or (2) must it be regarded as a later and relatively specialized property, achieved independently in two or more, perhaps many, phylogenetic lineages and therefor convergent in a number of modern groups? In recent papers Boyden (1953, 1954) has taken the latter stand in a rather extreme form. (It is extreme not only with respect to the concept of *sexuality* adopted here, but even with respect to the much narrower definition of *sexual reproduction* adopted by him—namely as "reproduction involving gamete production.") I favor the former stand, also in an extreme form—in fact, in its most extreme form—namely, that the evolution of sexuality as it exists today was the result of a single phylogenetic sequence. Hutner (1955, pp. 11-12) has already hinted at this idea in observing that "sexuality and the essential genic functions of a nucleus may already have evolved before the phytoflagellates and protozoa appeared."

The origin of sexuality has received but little attention from the principal students of evolution. Thus, Huxley (1942, pp. 85-86) discussed the evolutionary advantages of sexual mechanisms, but did not speculate on the conditions under which these mechanisms first arose. (To be sure, sexual phenomena in both bacteria and viruses were still unknown at that time.) Recently Haldane (1954, p. 20) has presented, in passing, some ideas on the sexuality of very primitive organisms —ideas that essentially say in a few words what I am presenting in a much more elaborate form here. Boyden is the only biologist known to me who has sought to answer these problems directly; although his major contention that primitive organisms were asexual for a vast period has been effectively refuted by Haldane, his exposition of the problem has made my own speculations much easier.

It is the primary purpose of this paper to present the viewpoint of the primitiveness of sexuality by assembling and analysing data on modern-day forms that make logical the extrapolation[3] of all present-day sexual mechanisms back to a common ancestral condition of primitive sexuality in the common ancestral group of all present-day organisms. In making phylogenetic reconstructions this process is often not verbalized, for the usual way of formally presenting them is in the reverse order—by beginning with the earliest stage that one chooses to consider and following the changes that one assumes to have occurred as any given type evolved into a later type or types. But, if the origin and significance of sexuality are to be analyzed adequately, I believe that one is forced to an explicit consideration of the most important points of modern evidence before a phylogenetic reconstruction can be satisfactorily attempted.

The question of the phylogenetic origin of sexuality is one of particular interest at the present time because we are seeing an eruption of discoveries on the genetic systems, including sexual mechanisms, of primitive organisms—protists, bacteria, and viruses. We are also witnessing important advances in our understanding of the gene—its biochemical nature, its immediate functional role in the cell, and its long-term role in the transmission of hereditary information in both asexual and sexual reproduction. All these discoveries provide a rich factual basis, hitherto meager, for speculation on the origin of sexuality.

The balance of this paper is therefore organized into two major sections—the first dealing with a necessarily brief analysis of certain fundamental information

[3] In connection with attempts to hypothecate some of the features of evolution at the primitive stages of life, Boyden (1953) has emphasized certain limitations of the method of extrapolation and contrasts it with the "method of direct assumption." Actually I believe that direct assumption is implicitly involved in all phylogenetic reconstruction—increasingly as the clues from modern forms and from the fossil and geochemical records are limited in what evidence they can provide. But I feel that extrapolation from available data—biological, chemical, and physical—in the real world is inescapably the foundation for all phylogenetic speculation.

on sexual mechanisms, some of it very recently obtained; and the second applying this information to a largely new synthesis—the postulation of the circumstances whereunder sexuality arose and of the earlier sequences whereby it evolved ultimately into the many sexual mechanisms in existence today. It is not possible to give in such a paper as this the detailed experimental and observational data from which the views here advanced are derived. I am indebted to a large number of published works, among which certain basic ones should be cited: these are semi-popular articles by Pollard (1954) on the physics of viruses and of Crick (1954) on the structure of DNA; the A.A.A.S. monograph on *Sex in Microorganisms,* 1954; and particularly the superb chapter by Luria (1953) on the origin and nature of viruses in his text, *General Virology.* In addition, a number of colleagues have been very helpful in discussing the ideas here presented. Of these, I am above all indebted to my friends, Drs. Spencer W. Brown, Victor Nigon, and Harold T. Gordon—to all three for making certain vital suggestions and for critically reading the manuscript; and to the last for the indispensable background of his many, as yet unpublished ideas on the nature of primary evolution, and for the constant stimulus of his constructive criticism, without which this paper would not have been possible. As is to be expected, we four have not agreed on all points, and I assume responsibility for the ideas herein expressed.

The Fundamental Features of Sexuality in Modern Organisms

Occurrence of sexuality. Phenomena that, by the definition of sexuality adopted here, must be regarded as sexual are now known for each of the major groups of living organisms.

It is desirable to digress briefly at this point and explain what I mean by "major groups"; they are four—the Monera (bacteria, blue-green algae, and certain related, presumably derived forms), Protista (protozoans, the "higher" algae, and all fungi), Metaphyta (higher, mostly terrestrial plants), and Metazoa (the multicellular animals). The boundaries between these groups are arbitrary, and their recognition is dictated out of convenience.

Boyden (1953, 1954) has expressed the belief that the major groups of organisms —"Protista" (in which he apparently lumps the Monera and Protista as constituted here), Metaphyta, and Metazoa—each had an independent origin from nonliving systems of biochemical evolution, that therefore the evolution of mitosis, meiosis, and sexual mechanisms was independent and convergent in these groups, and that furthermore the acquisition of sexual reproduction (as he defines it) was rather late—in fact even after the separation of the major phyla in the case of the Metazoa. The idea that in each of the three groups mentioned there were separate sequences of metatropy from the non-living to the living state is most assuredly a misconception. This is an inescapable conclusion, I believe, when many fundamental known facts of comparative biochemistry are considered—and even of comparative morphology. The devastating weakness of Boyden's presentation of his case for a polyphyletic origin of the major evolutionary lines and hence, inevitably, of sexuality lies in his failure to concern himself with the monerans and protists, including their morphology, biochemistry, and genetics.

The most important features of the phylogenetic scheme for the known world that I hold most probable are here summarized in Figure 1, highly modified from a figure of Hutner and Provasoli (1951, p. 30). This phylogeny is discussed later in the present paper.

Sexuality in the Protista, Metaphyta, and Metazoa. Insofar as is now known, in the protists and higher organisms those processes that are sexual by the definition adopted here always involve complex nuclei, within which the hereditary material is set off from the rest of the cell and organized into chromosomes. The phenom-

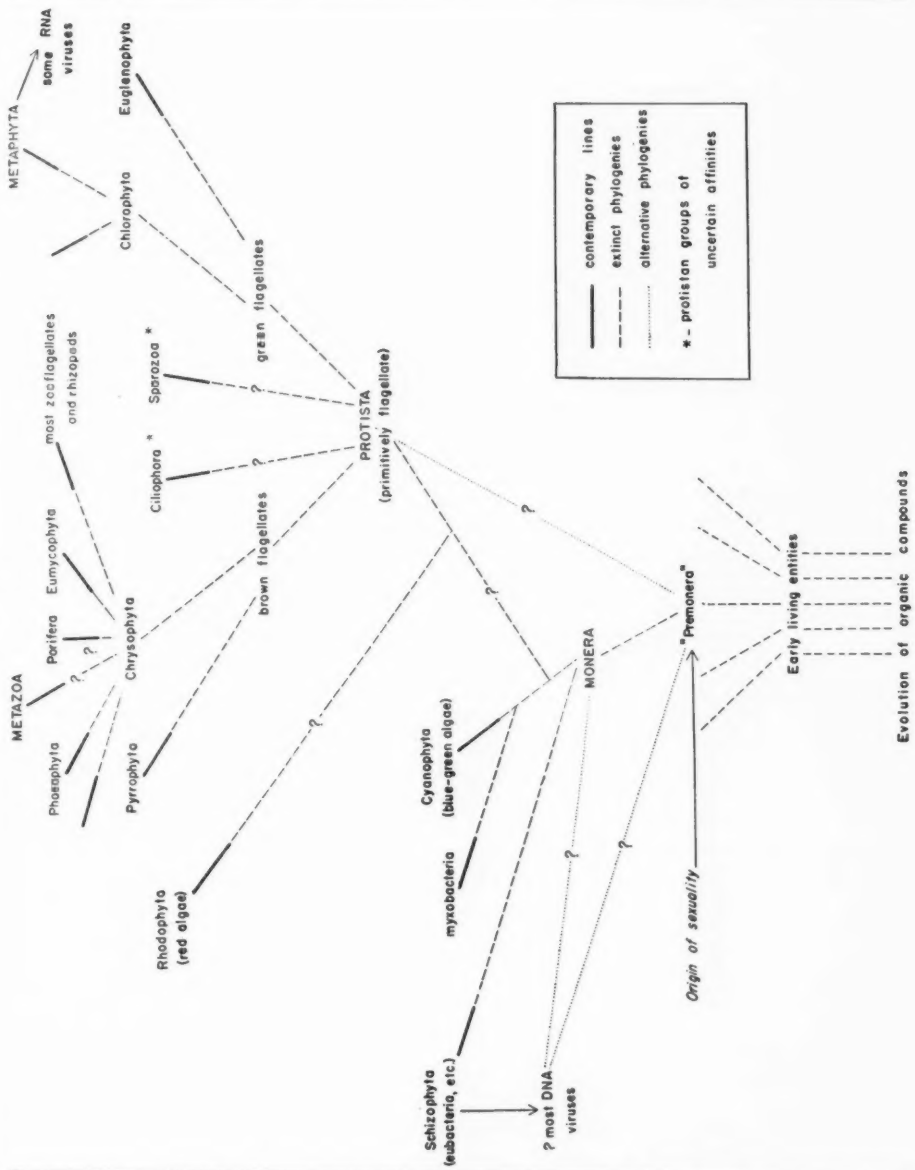

FIG. 1. Suggested phylogeny of contemporary living groups (highly speculative!), with the four "major" groups in capital letters. The solid lines leading to or from extant groups are not meant to imply a single metatropic (evolutionary) sequence, but rather to comprise *all* lines within each group. The algal phyla are those of Smith (1955) except as explained in the text. (If DNA viruses are dissociated gene-products, they conceivably can have arisen from nuclear material of all cellular groups. The RNA viruses—such as those of angiospermous plants—are here considered to be dissociated cytoplasmic particles.) (Figure much modified from Hutner and Provasoli, 1951.)

ena of sexuality can be rather precisely correlated with cytologically demonstrable structures and processes.

Sexual transfer mechanisms in these groups are characterized by the transmission of entire nuclei. This is usually accomplished by the fusion of pairs of specialized cells, the gametes, which are as a rule well differentiated in appearance from vegetative (somatic) cells and from each other in multicellular organisms, but are sometimes identical to, or little different from, one another in appearance in the unicellular protists. However, true conjugation, in which cells unite and then separate, often exchanging nuclei reciprocally, occurs in the Ciliata (see Wenrich, 1954*a*), which in agreement with Corliss (1955) I hold to include the suctorians, but not the "protociliates" (= flagellates). In addition, in protists such as the higher Eumycophyta, or fungi, fusion of cytoplasm, involving nuclear transfer, may take place between cells that are usually regarded as somatic (see, for example, Pontecorvo, 1953).

Recombination mechanisms in the protists and higher organisms are linked with the alternation of diploid and haploid numbers of the chromosomes within the nucleus, haploidization being effected by meiosis and diploidization usually by fusion of two haploid nuclei, although sometimes by doubling of a haploid set of chromosomes within a single nucleus. Normal meiosis not only segregates the diploid number of chromosomes into, as a rule, two homologous (or identical) haploid sets, but also usually permits the reciprocal exchange of chromosomal segments as part of the process of pairing of homologous chromosomes. Rarely, the haploid or diploid phase may be lost—phenomena associated, if gametes are still formed, with the invocation of various parthenogenetic mechanisms.

The cellular events that take place in association with nuclear cycles—especially of certain protistan groups—are highly diverse. These are most complexly elaborated in the higher algae—especially the Chlorophyta, or green algae (see Smith, 1955; Papenfuss, 1955)—and particularly in the fungi (Raper, 1954). In certain organisms belonging to these groups, fusion of two haploid nuclei into the diploid nucleus of a zygote may be followed immediately by meiosis and the reëstablishment of haploidy. The two meiotic divisions of the zygote nucleus are usually unassociated with cellular divisions, and three of the four resulting nuclei degenerate within the cell. At the opposite extreme are those algae and fungi that, like most metazoans and higher metaphytes (unless polyploid), have diploid nuclei except for a brief sequence following meiosis (usually a few nuclear divisions—as in the gametophyte generation of higher plants, but sometimes (as in certain yeasts) even restricted to a single nuclear generation—as with the gametes of most otherwise diploid metazoans). Intermediate are forms with a significant haplophase alternating with a significant diplophase in their life cycles, sometimes both phases being relatively long and elaborate.

A condition, unique to the fungi so far as is known, is *dikaryosis*, in which two nuclei, brought together into one cell by the fusion of gametes, remain associated, but do not fuse until a considerable part of the life cycle of the organism has transpired. A variant phenomenon, *heterokaryosis*, also occurs in fungi, in which somatic hyphae fuse and nuclei of different origin and thus sometimes of rather different genetic properties come to occupy the same cellular compartment. Present evidence appears to indicate that this is only rarely followed by nuclear fusion; thus the genetically different nuclei are generally segregated out from one another whenever uninucleate spores are formed. However, in some cases (see Pontecorvo, 1953), two such genetically different haploid nuclei may fuse into a diploid nucleus, in which in turn the chromosomes may undergo crossing over in mitosis, rendering certain gene pairs homozygous, or in which random distribution of chromosomes may occur at mitosis, sometimes with the reconstitution

of a functional haploid nucleus containing recombinations of the chromosomes of the original fusing haploid nuclei. Thus, in "somatic" tissue there is accomplished exactly what the more typical processes of "sexual reproduction"—fertilization and meiosis—are designed to do on a more regularized basis.

Despite the great variety of transfer mechanisms and the widely different cellular phenomena associated with recombination, the primary feature that unifies sexuality in the entire protistan assemblage and its descendent lines is the universal occurrence of *meiosis* as the means of effecting genetic recombination. Meiosis, of course, depends upon chromosomes and their ability to unite in homologous pairs and then segregate. Insofar as present knowledge indicates, meiosis in the protists, metaphytes, and metazoans always starts with the full chromosomal complement of a nucleus; except in fungal heterokaryosis and in genetic mosaicism of multicellular plants and animals, all participating diploid nuclei are genetically the same before meiosis (except as mutations occur) and contain almost all the hereditary determinants of an organism.

Sexuality in the Monera. Moneran sexual processes, which are as yet but little explored, provide a striking contrast to those in the protists, metaphytes, and metazoans. The most important difference is that, in sharp contrast to the practically universal rule for the latter groups, there is no case as yet found in which a moneran sexual process has been unequivocally demonstrated to involve the transmission of an *entire* nucleus. In fact, in many known cases only a very small part of a "fragmented" genome may be transferred. Thus, moneran sexual mechanisms involve a range of phenomena different in certain fundamental respects from, and presumably simpler than, those of the protists and higher organisms. Moreover, because of the much smaller nuclear apparatus and other cellular organelles of monerans, there has as yet been very little correlation of sexual phenomena with cytologically demonstrable structures and processes. Most of the phenomena now essentially accepted have had to be largely or entirely inferred from genetic data.

Transfer mechanisms are exceedingly varied. At the one extreme it is possible to introduce hereditary material into cells of a given strain of a bacterial "species" by treating them under special conditions with a "transforming principle," which on the basis of convincing evidence can be provided as a purified, essentially protein-free DNA preparation (Ephrussi-Taylor, 1951; Luria, 1953, pp. 351-2), derived from cells of another strain of the same "species." At the other extreme, the conjugation of two intact cells, resulting in genetic transfers, has been directly observed in living cells (Lederberg, 1955, p. 89; see Lederberg and Tatum, 1954, for a review of earlier inferential evidence)—and even the fusion of cells (Hutchinson and Stempen, 1954), although the genetic consequence of this latter phenomenon is not yet clear. Intermediate between these molecular and cellular phenomena is the transfer, between bacterial cells, of viral particles, which can effect various hereditary changes in the newly "infected" cells (see Luria, 1953, pp. 352–4; Jacob, 1954, 1955; Lennox, 1955; and others). Certain features of this are discussed in the next subsection.

Sexual recombination, just as sexual transfer, is exhibited at various levels of complexity in bacteria. Thus, Ephrussi-Taylor (1951) has found that, if a suitable strain of pneumococcus is infected with more than one kind of transforming principle, each differing in two or more respects from the others, some of the resulting transformed bacteria exhibit genetically stable *new combinations* of characters, which can only have been derived from different DNA molecules, or molecular aggregates. Transforming principles isolated from clones showing such recombinant characters are found to demonstrate these new combinations. This suggests a type of linkage of characters *within,* and an exchange of parts *between,*

DNA molecules. Similar phenomena occur with bacteriophages and are discussed in the next subsection.

Recombination mechanisms of a more elaborate sort are known in the intensively studied *Escherichia coli* (syn. *Bacterium*[4] *coli*), which is the only moneran so far shown by direct observation, *plus genetic corroboration,* to have strains that conjugate. The *E. coli* nucleus also exhibits exchange of linked DNA material within a single cell (see particularly the review of Lederberg and Tatum, 1954). After two sexually compatible, genetically different cells have conjugated and thereby exchanged nuclear material, a cellular line derived from one of the exconjugants can exhibit various recombinations of most genetic characters derived from both conjugating cells. (The other exconjugant shows much less recombination, however—Hayes, 1953.) It has been possible on the basis of statistical analysis of such new combinations to conclude that the *E. coli* genome is organized structurally into a very few linkage groups, possibly only one, analogous to the protistan chromosome (Lederberg and Tatum, 1954; Clowes and Powley, 1954). The nuclear bodies in this species, of which there are typically four (Ryan and Wainwright, 1954), appear each to consist of one, or a few, "chromosomes" in the *haploid* state. It is possible to interpret the nuclear behavior associated with conjugation in *E. coli* as involving the pairing of these "chromosomes," or of parts thereof, and the exchange of linked "genes"—a wholly or partially diploid state thus being established, followed by segregation. This process is therefore analogous to meiosis in higher organisms and may well be homologous with it, differing importantly, however, in that the bacterial "chromosome" is capable of "fragmenting" into subunits, which to a certain extent may behave independently of one another.

The mechanisms of moneran sexual recombination are still rather obscure, even for *E. coli.* The striking thing about these processes is that, unlike the nucleus in fertilization and meiosis in the great majority of higher organisms, the nuclear bodies of monerans have in no case been unequivocally shown, at least as yet, to follow a strict pattern of alternating haploidy-diploidy. In *E. coli,* the fusion of haploid nuclei to form a diploid nucleus, followed immediately, in most strains, by a meiosis-like process to reëstablish haploidy, appears to involve the regular elimination of part of the genome of one parent—a phenomenon with few known parallels as a regular event in higher organisms (see White, 1954, chap. XIII, for discussions of somewhat comparable situations in insects—especially in the dipteran genus *Sciara*).

In fact, it seems rather likely that not only the meiosis, but even the mitosis that occurs in the monerans is of a different type from that of higher organisms (Bradfield, 1954; Fitz-James, 1954). These views are, however, based on the study of but a few forms, and generalizations based on them must be taken with caution. Nevertheless, the purely morphological studies of moneran nuclei, having revealed a similar degree of simple morphology in many groups (see Bisset, 1950, for the eubacteria; and Cassel and Hutchinson, 1954, for the blue-green algae), suggest that a measure of agreement in mitotic and meiotic mechanisms may be expected. Some of the cytological aspects of bacterial mitosis and associated phenomena are now the subject of rather bitter controversy (Bisset, 1953; DeLamater, 1954), and for this reason can scarcely be used to support theoretical speculation.

Among others, Stanier (1953), if one may judge by his chapter on ". . . Darwinism among the micro-organisms," would speak of some, at least, of the foregoing phenomena as "non-sexual." This is, of course, a matter of definition, but I

[4] The International Committee on Bacteriological Nomenclature first conserved (1951), but more recently has rejected (1954) the nominal genus *Bacterium* Lehmann and Neumann, 1896, with type *coli* Migula *in* Engler and Prantl, 1895. The correct name for this taxonomic genus is now *Escherichia* Castellani and Chalmers, 1919.

feel that, viewed carefully, the distinction between what is "non-sexual" and "sexual" by any more rigid definition than what I have proposed becomes very difficult, and that for philosophical reasons all or almost all DNA transfer and recombination mechanisms in the Monera should be viewed as part of a single broad spectrum of primitive sexual phenomena.

Sexuality in bacteriophages and its relation to that of bacteria. Of all the work on genetic mechanisms, the study of the bacteriophages (or phages)—particularly the lysogenic and T- phages of *Escherichia coli*—has presented sexuality in very simple terms. Such remarkable advances in our knowledge of the genetics of these entities have been realized in the past decade that a whole new and important branch of biology has arisen. All but the most recent studies have been reviewed by Lwoff (1953) and by Luria (1953). Vital additional information is provided by Visconti (1954), Pollard (1954), Jacob (1954, 1955), Lennox (1955), and others.

Whereas the earlier observations on the biological properties of phages gave them the character of destructive parasites, it is now clear that many, perhaps all bacteria contain "prophages," which may derive by infection with "temperate" phages, yet appear to be parts of the bacterial "chromosomes, being entirely undetectable by most methods used in observing "typical" (virulent) phages, but under certain conditions capable of manifesting their existence—even becoming transformed into virulent entities. The intimate connection between some phages of *E. coli* (and also of related enteric bacteria) and the hereditary material of these bacteria themselves is becoming increasingly evident, and now it seems more than a mere speculation that bacteriophages (or at least prophages) may be an integral part of the bacterial life cycle—gene products that are potentially capable of transmitting genetic information between bacterial cells—and that a virulent phage is an exceptional one, with which the sensitive "host" bacteria are in a biological imbalance.

But, because the idea of bacteriophages as parasites of phylogenetic origin independent from that of their bacterial hosts is still a common one and, indeed, cannot as yet be said to have been disposed of, one cannot, at least as yet, logically treat their "sexuality" as a special aspect of the sexuality of the bacteria in which they occur.

If one views bacteriophages as entities separate from the bacteria inhabited by them, then they do not, in a strict sense, exhibit sexuality as defined here. It is true that, when "matured," they have their own simple "cellular" compartments and are capable of effecting transfer of their DNA from one such compartment to another and of undergoing recombinations in the process. However, these mechanisms of transfer and recombination are in certain respects different from those already discussed. The compartment of the phage is a protein envelope, which is made in the bacterium in which the phage matures; and, when the latter is liberated and enters a new bacterial cell, this envelope is left outside, and little if anything more than the DNA slips inside (Hershey and Chase, 1952). The reproduction of, and recombination processes between, phage DNA molecules then go on inside the bacterial cell before new protein envelopes are formed around individual phage DNA molecules or molecular aggregates (or possibly pairs thereof—see Levinthal, 1954).

Therefore, the DNA transfer mechanism of a single phage—from one protein envelope to the many of its descendants—is analogous to vegetative reproduction in monerans and higher organisms.

However, the DNA recombination mechanisms of phages are such as to justify the extension of the concept of sexuality to them and have, without any doubt, great significance to the discussion here. Thus, two or more related coliphages, infecting a single *E. coli* cell and differing by two or more hereditary properties, may give rise to genetically stable phages exhibiting new combinations of characters derived from the two or more par-

ental types. It has been possible to show that certain of these characters are linked in linear sequence and that possibly the mature phage contains a single DNA macromolecule (or a pair of homologous molecules); thus, the explanation of recombinations of linked characters appears to be that even in vegetative reproduction two phage molecules pair and exchange parts. Critical mathematical analysis, by Visconti and Delbrück (1953), of the results of mixed infections has led them to the conclusion that the mature phage is the product of several rounds of mating and exchange of parts (an average of five in coliphage T2).

If we now add to this picture the phenomenon of "transduction," whereby lysogenic (temperate) phages (see particularly Jacob, 1954, 1955; Lennox, 1955) are capable of acting as genetic vectors for the transfer of a wide variety of properties between related strains of bacteria, there emerges the clearest evidence of an intimate connection, in these cases, between phage and bacterial genome.

If we thus assume for the sake of argument that bacteriophages are not independent parasites, but semi-autonomous gene-products of bacterial nuclei, then they well qualify as part of a sexual transfer mechanism, especially in vectoring genetic properties; and the ability of their DNA molecules to pair and exchange parts constitutes for the bacteria a sexual recombination mechanism of a very simple type—quite possibly identical with that already mentioned as exhibited by bacterial transforming principles. In this context, a statement of Luria (1953, p. 208) gains particular significance: "It might even be that every portion of the genetic material of a bacterium has some potentiality to mature into a transmissible agent, that is, to become a phage."

In view of the widespread occurrence of bacteriophages and their intimate connection with the bacterial nuclear apparatus, I feel that it is a more reasonable view to regard them as semi-autonomous entities derived from bacterial nuclear material rather than as parasites of long independent phylogeny. This does not preclude their having had a degree of independent evolution, but suggests that they are homologous with parts of the chromosomes of their bacterial "hosts." The picture is not a simple one, however, for certain of the T- phages, unlike temperate phages, have a pyrimidine base—5-hydroxymethylcytosine (combined, remarkably enough, with glucose—Sinsheimer, 1954)—not otherwise found in *E. coli*. It seems rather likely that these differ from the lysogenic phages and are only remotely related to the *E. coli* genome—perhaps are intruders from some rather different moneran genetic system.

The molecular basis of sexuality. Merely to establish that there are sexual mechanisms in organisms ranging from bacteria and their viruses up to the most complex metazoans does not of itself constitute proof that these many processes derive from a common ancestral state. However, one has but to look at the chemical nature of the hereditary material itself to be led to this as a reasonable hypothesis.

Although indirect for the most part, there has long been evidence, of which certain impressive features have only recently been elucidated, that one class of chemical entities, which are universal constituents of chromosomes as well as of the larger viruses, are the basic repositories and transmitters of hereditary information and thus are the principal regulatory stuffs of life. These are the DNA's (desoxyribosenucleic acids—also known as deoxyribose- (or -ribo-) or des- or deoxypentose (or -pento-) nucleic acids!). A theory of the polyphyletic origin of life, such as Boyden's, would almost certainly demand that these complex molecules have been independently evolved as many times as there are independent lines. This impresses me as a very strained concept indeed.

The role of the DNA molecule in transmitting hereditary information is most clearly and simply manifested by the bacterial transforming principles and the bacteriophages. It may well be argued

that generalizations from these two highly specialized cases of DNA behavior are suspect. But one cannot, I feel, escape the reasonable inference that these DNA's are representative of all DNA, and that it is precisely because it is possible to isolate them entirely, or largely, from their cellular environment and—unlike the DNA of higher cells—to reintroduce them in a controlled way, that one can illustrate clearly the hereditary role that they presumably share with all DNA.

Recent work, which it is beyond the scope of this paper to review in detail, has established a probable structure for DNA (see Crick, 1954; Feughelman *et al.*, 1955), which has been hailed by a number of geneticists (*e.g.*, Beadle, 1955) as providing a good working model for explaining genetic heritability on a molecular level. A DNA is a macromolecule consisting of a double helix of two polynucleotide strands bound linearly by phosphate diester bonds and kept in apposition by the hydrogen ion bridging between specifically paired purine and pyrimidine bases. Particularly with the concept of this structure in mind it is, I feel, possible to essay an explanation of the origin of sexuality.

The Origin and Evolution of Sexuality

The primitive sexual organism. I have already taken the position, in the introductory section, that currently existing sexuality as here defined arose as the result of a single phylogenetic sequence. The reasons for this should now be explained.

In order to suggest a stage in the evolution of life at which this origin most logically could have taken place, one should ask the question, What common properties of living systems must be used to extrapolate back most reasonably to a common ancestral condition as regards sexuality?

From the discussion of the preceding section and the definition of sexuality given in the introduction, it is obvious that a *sine qua non* of a primitive sexual organism as conceived here would be the possession of DNA as its fundamental hereditary material. However, no one can reasonably pretend that a DNA is a primitive compound. Such a compound almost certainly could not have come into existence as a regular substituent of a living system until a considerable part of the primitive metabolic machinery was established—in other words, in entities that had already undergone a significant amount of evolution in a state that could reasonably be conceived of as living. I hold that the evolution of the DNA structure was a very complex and intrinsically unlikely thing—that it was a later one of the relatively few successful results out of countless numbers of chance experiments of all kinds in early biochemical evolution.[5]

A second feature that I hold necessary for entities in which sexuality could have evolved is that they must have had some sort of primitive cellular structure—in other words, that they were organized as compartments limited by a cellular membrane and containing a primitive sort of protoplasm with a primitive metabolism. I believe that DNA could not have arisen except within such a limited system. To defend this belief adequately is outside the scope of the paper, but it should be stated that my concept of the earliest stages of biochemical evolution, as derived essentially from unpublished views of Harold T. Gordon, are fundamentally involved in such a view. Independently and for somewhat similar reasons Lanham (1952) has also argued that nucleic acids could not have been present in the most primitive cell-like systems.

Given these two features—DNA in a

[5] On this theory, living systems consisting of, or containing, such advantageous innovations would tend to overrun the rest, and, after a number of such cycles, all surviving organisms would inevitably be the descendants of a single living line of a somewhat earlier period. This is a variant of the "rare accident" theory, which Boyden (1953) correctly criticises if it is to mean that life began by the chance assemblage of a tiny bit of protoplasm, from which all subsequent forms have descended. Boyden is arguing against an oversimplified concept, however.

cellular compartment—which are common to all living systems (even including the viruses when growing in their host cells, the RNA viruses being then in the presence of the host DNA), one would have, I believe, all the necessary features for the evolution of sexuality. Furthermore, one would also have a group of organisms that could serve as the common ancestor of both the moneran line (and through them, in all probability, some, possibly most, of the viruses) and the protistan line (with its metazoan and metaphytan offshoots—and the balance of the viruses). But even the least complicated living members of these two major lines, moneran and protistan, are far from being simple organisms; and it is thus obvious that at least two great sequences of more primitive forms, deriving from an earlier single line ancestral to the Monera and Protista, are represented in the contemporary living scene only by their highly evolved descendants. Furthermore, it seems a wholly reasonable conclusion, if one may judge by the pattern of evolution in those groups having a fossil record, that contemporaneous with, and paralleling, the particular ancestral group common to the Monera and Protista, there must have been other groups of fundamentally less adaptable and generally more primitive structural types, which left no direct descendants at all.

For a number of reasons the modern Monera, though they are highly evolved organisms in their own right, may, I believe, be taken as preserving more primitive features than the Protista and thus may be considered as closer to the hypothetical ancestor in question than are the latter. Because of this, I feel that one may usefully speak of the common ancestor as representing the *premoneran* level of organization and of such organisms as constituting a hypothetical group, the *Premonera*. It therefore follows that, in attempting to reconstruct the probable conditions under which sexuality arose, one must look to the bacteria and their viruses for clues.

It can be argued that, since the sexual processes so far observed in the Monera (transfer mechanisms—such as transformation by DNA, transduction by viruses, conjugation, and possibly cellular fusion—and recombination mechanisms) appear to be rare phenomena, produced under special laboratory conditions in a few eubacteria and viruses (and not discovered, at least as yet, in the blue-green algae and myxobacteria), they do not necessarily represent an ancient property of the Monera, but rather in all likelihood are emergent in a few bacterial groups. This argument can be extended further by pointing out that bacteria and blue-green algae are seemingly capable of indefinite vegetative reproduction and that, therefore, to expect sexual mechanisms to be characteristic of the Monera as a whole is not warranted.

There can be no definitive rebuttal of such a viewpoint so long as relatively little is known of the range of sexuality in the Monera. But it would seem to me that a better explanation for the occurrence of sexual mechanisms in the very forms in which they have been systematically sought is that the modern Monera have perfected a system of very rapid vegetative reproduction, combined with a nonmutational variability (particularly evidenced by their ability to make adaptive enzymes)—properties that have subordinated in importance sexual mechanisms that would have been far more in use by less efficient, more slowly growing organisms. On this view, the demonstration of sexual mechanisms in bacteria serves as evidence for an ancient common sexuality in the Monera and their ancestors; indeed, the very fact that these mechanisms exist at all would suggest that, as efficient as the bacteria are in their vegetative reproduction, they still encounter, in a state of nature, special conditions under which a sexual mechanism is sufficiently important to play a decisive role in the survival and success of the species. If this view is correct, it seems to me to lead to the prediction that in time most, probably all, the Monera will be shown to rely on sexual

mechanisms of one sort or another, at least under special environmental conditions.

The nature of moneran sexuality, characterized by fragmentable genetic systems of DNA, which exhibit the ability to exchange molecular parts, points to the most likely type of premoneran in which sexuality could have arisen. Such an organism would be a small cellular compartment harboring at least several DNA molecules, which would resemble one another to varying degrees depending upon the extent to which duplication of a given molecular species had been perfected, the number of that species that could, or had to be present, and the number of kinds of more or less independent species that had developed within the cell before sexual transfer mechanisms evolved. Its vegetative reproduction would in all probability have taken place by budding, with a more or less random distribution of DNA molecules between the mother and daughter cells (much as plastids are distributed when modern cells containing them divide).

It is probably of little value to speculate further on the population of DNA molecules in such a system, but it is worth remarking that, if each member of the population were significantly different from the rest (as would be true if imperfect duplication were the rule and as I believe was primitively the case), then it would, I feel, be undesirable to think of them, as does Boyden (1953, 1954) as *polyploid*. Polyploidy denotes the presence of three or more identical, or nearly identical, complete sets of all genetic units within a cell. The organisms here under consideration would be better characterized as exhibiting a primitive sort of *heteroploidy*. Such a system can provide a logical basis for postulating *why* sexuality arose, as I now propose to detail.

Why sexuality arose. An effort to explain the origin of sexuality makes desirable the separate consideration of its two essential aspects—namely, transfer of DNA molecules, or aggregates of such molecules, *between* (or *among*) two (or more) separate compartments; and the recombination of DNA molecules, or aggregates thereof, by their being sorted out and by their exchanging parts between (or among) one another *within* a cellular compartment. Although both of these processes are necessarily involved in any transfer mechanism for the reason that the introduction of DNA into a new cellular compartment in itself establishes a new combination within that cell, recombination mechanisms most probably arose in their simplest form independently of, and earlier than, transfer mechanisms in evolution.

Recombination mechanisms could be said to have had their primitive beginning as soon as cellular compartments had developed more than one species of DNA and these species began to compete with one another as occupants of the cell. In a simple, presexual organism, regulation of genetic balance might well have been achieved by the differential reproduction of DNA species within the cell. Such balance could also have been maintained or changed by the selective destruction or elimination of certain molecules. It seems necessary to assume that the capacity of a cell to tolerate a certain degree of variability in genetic content would have to be present before such a system could accept and integrate into its hereditary framework genetic units derived from other compartments. But, until the advent of regular (hence sexual) DNA transfer mechanisms it is hard to imagine that there would have been much evolutionary pressure toward a system of recombination more complicated than differential growth or destruction of competing species of DNA molecules.

It is nevertheless conceivable that the ability of DNA molecules to pair and exchange parts arose at a time before transfer mechanisms had evolved. Consider the advantages of such a property in a closed system of relatively few DNA molecules: two or more damaged molecules, or aggregates, could pool their undamaged parts and reconstitute an intact

unit (as has been suggested as occurring under certain circumstances in the case of bacterial viruses damaged by ultraviolet irradiation—see Luria, 1953, p. 195), and two macromolecules, or aggregates, each possessing a new and improved substituent part, could effect new and desirable combinations. In a closed system of relatively few molecules, the first of these factors would seem to be the more likely as an evolutionary cause for the emergence of molecular pairing and exchange.

I do not, however, consider molecular recombination and exchange within a closed system to be a *complete* sexual process. It could become *part* of a complete process only when DNA transfer mechanisms had been developed and regularized. As regards the latter, it seems likely to me that they were very early achieved by the primitive premoneran.

It is, of course, possible to imagine that the most primitive organisms reproduced without any transfer mechanisms at all, as here defined. But consider their limitations. These fall into two categories: first, such an organism would be unable to replenish from an outside source its necessary complement of DNA molecules if any essential species of molecule were destroyed within it, or, put somewhat differently, the DNA molecules of a fatally damaged cellular compartment would have no way to survive the destruction of their cell; second, a new and advantageous DNA species would be limited to the descendants of the cell in which it arose—that is, there would be no way in which such a species could be transmitted to other cellular compartments already separated from the originating cell, and thus there would be no way for two or more different, new, and superior DNA species arising originally in separate cells to coexist within a single cell except by multiple independent origins of each new species.

Now consider the situation in which a transfer mechanism does exist. First, cells in which an essential DNA species is damaged or destroyed have a potential way of correcting the defect by assimilating a replacement from other cellular compartments; or, put somewhat differently, DNA species of a damaged or destroyed cellular compartment have a way of avoiding extermination by finding and taking up residence in new cells. Second, new and desirable combinations of better DNA species arising in separate compartments do not have to await independent events in each line of cellular descent. These two factors are thus extensions of the same two that have already been considered in connection with pairing and exchange between DNA molecules.

Probably it is impossible to decide which of these factors was the critical one in establishing regular DNA transfer mechanisms in the evolution of the premoneran—that ensuring survival, or that promoting progressive properties. On the basis of evidence from modern organisms the metatropologist would, I believe, tend to favor the latter interpretation, but the situation as regards the premonerans may have been very different from that characterizing such of the modern monerans and most primitive protists as have been analysed. These present-day forms are striking for their very rapid generation times and appear to have relatively infrequent need for mechanisms whereby a damaged DNA apparatus can be repaired with parts from another cell or cells, or whereby their DNA content can survive by finding a new cellular habitat. But, if by contrast the early premonerans reproduced themselves slowly and inefficiently, as would seem a not unlikely circumstance, then any mechanism of permitting survival of a DNA-deficient cell, or (and especially) of a DNA species residing in a fatally damaged cellular compartment, would have been highly favored, and the establishment of DNA transfer mechanisms by metatropic processes could have been importantly influenced, possibly determined, by such needs. It is possible to conceive of the ability to form desirable new combinations as the decisive factor in then regularizing DNA transfer mechanisms as

sexual processes. This last factor could then play its enormous role in progressive evolution.

The answer to the question of *why* sexuality arose in the primitive premoneran would therefore seem to be that closed cellular systems containing a heteroploid population of DNA molecules were necessarily limited entities. The ability of genetic determinants—DNA molecules—to transfer from one such system to another had great advantages, both in making repair and survival possible and in greatly accelerating evolutionary improvement.

How sexuality arose. If in the foregoing discussion a reasonable answer to the question of why sexuality could have arisen in the premoneran is provided, one is still confronted with the question as to how it took place.

A possible model of the first DNA transfer system, according to what might be called the "infection" theory [6] is the following: primitive organisms containing DNA molecules were subject to death and dissolution under sufficiently unfavorable conditions; in some cases—possibly rarely—their DNA was stable enough to survive beyond the destruction of the cellular compartment for a time; some of these were able to enter other cellular compartments, possibly by having appropriate associated enzymes; and finally in some cases the intruding DNA was able to adapt to, and grow in, the new environment.

We know that this is essentially what takes place in bacterial transformations today. Although it is true that those known require rather specialized conditions for the transforming phenomenon to occur, the fact that a DNA modecule, surviving free in solution, can enter a bacterial cell and there become a stable part of the hereditary material of that cell is a provocative suggestion for what may have been the earliest transfer mechanism. To those who may protest that to assume such a stability for primitive DNA is unwarranted, I can only reply that, if not present from the very first, then somewhere in the evolution of the Monera such stability *did* develop since it exists today; and it does not seem to me an unreasonable assumption that very early DNA may also have been relatively stable, possibly in combination with a primitive protein.[7]

I doubt that we can determine with present knowledge how intrinsically difficult the several steps in an "infection" transfer would have been for a primitive premoneran, but they constitute in my estimation one of the simplest theoretical sequences from which a sexual transfer mechanism could have been developed. For the transfer process to qualify as a sexual one as I have defined sexuality, there would be required only the *regularization* of the foregoing process so that it would become a constant and essential part of the life cycle of organisms possessing it—probably not with each duplication of the cellular compartment, but at least at some more or less regular period in the multiplication of the organism, or under certain recurrent environmental conditions, to which the organism would at times be inevitably subjected.

An alternative scheme for the first transfer mechanism—according to what may be called the "fusion" theory—is the following: two (or more) primitive premoneran cells came into chance contact; sometimes the cell-wall barriers between them dissolved—at least enough to per-

[6] Ravin (1955) has recently reviewed the "infective" properties common to viruses and genes without, however, explicitly extending this analogy to its implication for phylogeny.

[7] I might in this connection point to the remarkable fact that isolated and washed sperm nuclei of certain fish can apparently be used to initiate development of the corresponding egg (see Felix, 1955). The actual genetic participation of these nuclei has yet to be shown; but, if such does indeed occur, then the stability of DNA-protein outside of the cell is evident not only for the bacteria, but for some, at least, of the highly evolved metazoans! This would suggest a high order of stability to be a universal property of DNA (or DNA-protein). It should be admitted, however, that fish sperm nuclei probably retain a protective membrane containing lipoprotein.

mit mixing of some protoplasm, possibly the fusion of entire cells; DNA species were thus able to cross from one such cell into another, just as they might if the primitive process of vegetative reproduction of cells were by budding, as seems likely, and DNA molecules passed into the daughter bud more or less at random. We know that a process of conjugation occurs in *E. coli* and that cellular fusion has been observed in a number of bacteria. Again we can probably not know at present how intrinsically difficult these several steps would have been to a primitive premoneran.

Regardless of which of the two mechanisms—*infection* or *fusion*—arose first, both manifestly evolved, for both are represented in the modern Monera. It seems not unlikely that both developed at an early premoneran stage. These alternative theories of the first transfer mechanism are presented as Figures 2 and 3.

Formulating the simplest theoretical model for the phenomenon of intermolecular exchange of parts is perhaps simpler than formulating the simplest model for a DNA transfer mechanism. Certainly the structure of DNA as recently elucidated and its assumed means of self-duplication provide a reasonable basis for conceiving of intermolecular exchange as a partial reversal of the duplicating process. Thus, if in self-duplication the double strand of a DNA macromolecule can line up free nucleotides in two appropriate complementary sequences such that the esterification of the latter can take place, one may conceive of the orientation of two such double strands,

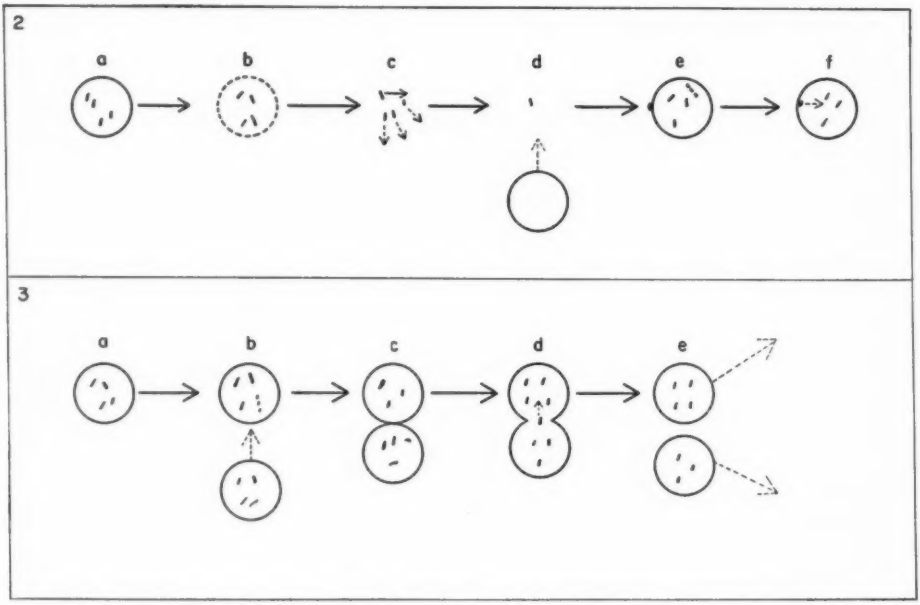

FIG. 2–3. Alternative schemes for the origin of primitive sexual mechanism. (Original.)

FIG. 2. The "infection" theory. *a*, hypothetical premoneran cell (schematic); *b*, . . . undergoing destruction; *c*, release of DNA molecules; *d*, surviving molecule approaching a new cell; *e*, . . . attached to cell; *f*, . . . having entered cell.

FIG. 3. The "fusion" theory (conjugation variant). *a*, as in 2*a*; *b*, a DNA molecule undergoing destruction while cell is approached by another cell; *c*, cells stuck together; *d*, cells partially fused, with migration of DNA particle from one into other; *e*, separation of cells.

already formed, as permitting the coming together of homologous parts of two separate molecules. It is not difficult to imagine that exchange may take place in the process of separation of two previously independent, but essentially identical double strands, which pair.

It seems a reasonable hypothesis to assume that in evolution self-duplication arose first and was followed later by the ability of similar or identical molecules to pair and exchange parts. That this ability was probably achieved in the early premoneran is strongly supported by the fact, already discussed, that it is known to occur between molecules of related transforming principles differing by two pairs of genetic markers and is found in bacteriophages.

One can only speculate on how this took place in evolution. If one assumes, as I feel one must, that the earliest DNA's were relatively simple by comparison with those of modern organisms, then they may have been actually so simple that a pairing and exchange reaction would have been of relatively little importance, either to restore damaged parts or to permit the establishment of superior molecules out of improved substituent parts of separate molecules. But, with the evolution of transfer mechanisms and of more complex DNA, the need for an orderly pattern of recombination can be perceived as becoming a necessity. It is reasonable to assume that the ability of DNA to pair and exchange parts, if not evolved before, would then be necessary. The fact that, by present evidence, the reproduction of bacteriophages within the host cell is accompanied by rounds of pairing of homologous phage molecules as an essential part of the duplication process is certainly of highest significance in this connection. It should come as no surprise if a comparable phenomenon is found to characterize the duplication of the bacterial nucleus also.

I am therefore here suggesting that *a pairing process of the bacteriophage type has been the evolutionary basis of all phenomena of DNA pairing found in modern sexual mechanisms.*

From the foregoing discussion, I am led to the hypothesis of a period in the history of life in which the most advanced organisms were tiny, primitive, protoplasmic sacs, which contained populations of DNA molecules, capable of moving from one such cellular compartment to another and of exchanging substituent parts with one another. Luria (1953) has speculated in a fascinating way on the evolutionary implication of virus-like bodies able to move in and out of cells and, in the course of evolution, to gain and perhaps lose again an intimate union with the original heredity of host cells. If one projects such ideas backwards to the premoneran level, one can conjure up a very fascinating stage of life. In such a world, the "virus" and the "gene" were one and the same—except that at the extremes one was a wanderer and the other a stay-at-home. If I may be permitted a flight of fancy, I will suggest that these early "viruses" not only transferred from one cellular compartment to another of the same type, but some of the more adaptable ones spread out and colonized other compartments of more primitive sorts, took up residence there, and molded their new homes and were molded by them into new forms. If this idea is true, then evolution of that time worked with a shifting population of virus-like entities moving back and forth, hither and yon, among the primitive cellular compartments—forming new combinations and deserting old.

We could conceive of evolution as occurring at this stage not as descent from a single line of cells, but as descent through populations of diverse cells in which the transfer of hereditary material between cellular compartments went on continually in an intricate way. The present-day ability of a given virus "species" to infect cells of long-separate phylogenetic history may be a modern counterpart of an analogous situation in a relatively early evolutionary phase of life when primitive cellular systems could be modified by the rare but decisive addi-

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tion, to their permanent hereditary content, of genetic material from long-separate cellular lines. It is even not unthinkable that some of these earliest viral entities survive in not-too-different form to this day.

The evolution of moneran sexuality. As regards sexual transfer mechanisms the modern monerans have preserved, as we have seen, a whole gamut ranging from the simple and direct infection of moneran cell with DNA particles to complicated processes of conjugation involving the transfer of most, possibly all, of the genetic content from one cell to another. Whereas it is not difficult to account for this range of transfer mechanisms as evolving from the hypothetical condition of the primitive premoneran, an explanation for the evolution of the associated recombination phenomena is less readily offered, partly because the picture of just what happens in such recombination is still far from clear.

The modern monerans, as exemplified by *E. coli*, being organisms with primitive, but nevertheless rather specialized nuclear bodies, which appear to be analogous to the chromosomes of higher organisms, are a rather far cry from the small sacs containing a heteroploid population of semi-autonomous DNA molecules that I conceive the primitive premoneran to have been.

But one is not entirely without a modern system that might be considered to approach more nearly the premoneran condition in this respect. For the sake of argument, let us consider as a model the bacterium-bacteriophage complex, where the phage is of virulent type.

If one disregards the bacterial nucleus, one has in such a system a gradation from simple haploidy (or possibly diploidy) when the cell is first entered to a high order of polyploidy, as regards the infecting DNA molecule, in the latter stage of vegetative phage reproduction—and all this within a single cellular compartment. Now I do not propose that this condition is more than approximately like that in the primitive premoneran, for the multiplication of a bacteriophage is obviously a highly specialized situation in a highly specialized cell. Nevertheless, this system is, I feel, not without implication for any consideration of the primitive premoneran state, for we know from the bacterium-bacteriophage model that a DNA species (or aggregate of species) can under certain circumstances be present in a wide range of numbers within a single cell.

It may be questioned whether, in speaking of the virulent bacteriophage as present in the *polyploid* state when it has grown at the expense of the host cell and in also speaking of the *E. coli* nucleus as *haploid,* one is actually using the concept of ploidy in an homologous way. The *E. coli* nucleus is certainly something more complex than the bacteriophage. Yet conceivably the former merely extends the same macromolecular structure to somewhat greater dimensions. Possibly, however, it is an aggregate of macromolecules somewhat similar to individual bacteriophages, these being united, however, in a linear sequence by bonding of a different and perhaps looser nature than the phosphate diester linkages of the DNA macromolecule. In either case, it is possible that there is within the bacterial nucleus a serial duplication of macromolecular units or subunits comparable to the bacteriophage. If such is the case, when viewed at the molecular level, ploidy in the bacterial nucleus and ploidy in the bacteriophage are not comparable.

What one must assume is that, in the evolution of the moneran state, heteroploid populations of DNA molecules were disciplined by the selective forces of metatropy into a system of haploid nuclear bodies. This certainly had to involve an increased complexity of the hereditary DNA and perhaps also the linking together of primitively separate DNA molecules into chains of such molecules, possibly by means of new kinds of bonding different from the phosphate diester linkage of the DNA macromolecule. The great advantage of having all or most genetic material in one or a few linkage

groups would lie in the ability of such united bodies to effect a more orderly partition of basic genetic material between two cells in vegetative reproduction.

Concomitant with the evolution of this more complicated nuclear structure, sexual mechanisms had to become more complex. The bacteriophages of lysogenic type may represent a sexual process evolved directly from the most primitive "infection" type of transfer mechanism; and conjugation in *E. coli* may represent a perfection of the primitive "fusion" type of transfer mechanism. As regards mechanisms of sexual recombination, it seems necessary to assume that the pairing ability of the early DNA molecules became the basis upon which the much more complex moneran chromosome could evolve "crossing-over" as found in *E. coli.* An adequate formulation of such sequences certainly awaits, among other things, further knowledge of the structure of the bacterial nucleus and especially of the behavior of such nuclei in sexual processes.

The evolution of protistan sexuality. The origin of protistan sexual mechanisms, and thus of metaphytan and metazoan as well, from the premoneran-moneran condition involves certain new and complex features not seen in the Monera. The derivation of the protistan type of nuclear organization can only be speculated upon at this time. However, it would appear that there is no basic fact so far known that would preclude one's regarding the protistan nucleus as derived from the moneran type—by the elaboration of the latter into a system of chromosomes organized into a discrete nucleus and the differentiation of new structures, such as the centrioles and spindle (or possibly their elaboration from already existing structures, which present cytological techniques are as yet insufficient to disclose unequivocally in modern monerans), making possible organized mitosis and meiosis.

There is still much to be learned of the nuclear and genetic systems of the simplest surviving flagellates. It may indeed be that the differences between moneran and protistan organization will be shown to be much less clear-cut when the "nanoplanktonic" flagellates, some of which are of the same dimensions as are the moderate-sized eubacteria (Butcher, 1952), are studied cytologically and when the possible existence of simpler sexual mechanisms than those involving meiosis and transmission of whole nuclei is thoroughly investigated. We already know of the widespread occurrence of viral DNA infections in cells of insects and vertebrates. Their occurrence in the Protista has not been adequately investigated, but at least one virus-like entity is known in a protist ("kappa" in *Paramecium aurelia*—see Wichterman, 1953; Beale, 1954). There is a distinct possibility that many such entities exist and that some are an intimate part of the genetic systems of the cells that they occupy.

In any case, sexual transfer mechanisms in the Protista and higher groups, as has been pointed out, involve whole nuclei, and thus the presumably more primitive type of exchange, wherein only a part of the genetic content of a cell is transmitted to another, has essentially been abandoned so far as we know. As with the Monera, I see no particular difficulty in deriving such mechanisms by progressive evolution of the Protista from the Premonera—probably through monerans in which cellular fusion already could occur (as in many modern bacteria). The fusion of gametes seems to me best explained as an elaboration of the ability of cells at the moneran level to fuse. Reproduction by the formation of gametes is the basic feature of sexuality in Boyden's hypothesis (1953, 1954). Unlike Boyden, I cannot in any way see gamete formation as a feature of late metatropic acquisition. Conjugation in the ciliates does not, however, impress me as directly descended from the primitive "fusion" type of sexual transfer, hence from the type of conjugation exhibited by *E. coli*; the ciliate process is rather clearly a specialized phenomenon, of which the

evolution was made possible by reason of the special surface structure of these organisms. Similarly, heterokaryon formation in the Eumycophyta is to be regarded as a special property of fungi. Nevertheless, all these phenomena seem to me to partake of a primitively evolved ability of cells to fuse, in part or in whole, and merge or exchange DNA populations.

As regards recombination mechanisms, the gap between the Monera and the postulated Premonera is perhaps greater than, or at least as great as, that between the Protista and the Monera. In the latter two groups vegetative reproduction involves an orderly equipartition of nuclear material between the two daughter cells—by mechanisms of mitosis or some comparable process. In both groups meiosis or some probably homologous process exists as a special variant of mitosis, in which the orderly association of chromosomes or chromosome-like bodies into homologous pairs makes possible the recombination of genetic properties and their orderly segregation.

Certain important differences between the known members of the latter two groups seem evident, however. Just as the bacterial "chromosome" is more complex than the bacteriophage DNA molecule, so is the protistan chromosome more complicated than the analogous bacterial structure and thus, of course, than the bacteriophage DNA molecule. If it is not clear whether the macromolecular structure of the virus DNA has simply been extended in the bacterium to much greater dimensions, it is even less clear that this is the manner by which the much more complex protistan chromosome has arisen. In fact, there is some evidence that such may *not* be the case. Mazia (1954) has reported the breaking of chromosomes from sperm heads of a species of sea urchin into small particles by a method including, as one step, the use of the chelating agent "versene" (ethylenediaminetetracetic acid), which is known to form complexes with calcium and magnesium ions. He has suggested a particulate nature to these chromosomes, in which the bonding between particles involves the participation of calcium and magnesium and is fundamentally different from the phosphate diester bonds that connect nucleotides in linear sequence in the DNA macromolecule.

For the foregoing reason the "crossing-over" that occurs when a bacteriophage molecule exchanges parts with another, and possibly also when the linkage of a bacterial "chromosome" is changed by association with a chromosome of different linked properties, may be fundamentally different from the true crossing-over that occurs in protistan, metaphytan, and metazoan meiosis. On such a supposition meiotic crossing-over in higher forms may involve separation between contiguous particles on each of two chromosomal strands, followed by reciprocal reclosure between particles on different strands. However, even if the particulate nature of the higher chromosome is a fact, it does not necessarily follow that crossing-over does not involve the same type of transfer of bonds that occurs in the lower forms. In fact, the biological unity of conceiving of all these processes as based fundamentally on the phenomena of DNA pairing and exchange is most attractive.[8]

Detailed phylogenetic speculation on the evolution of variations in the cellular events associated with sexual recombination mechanisms in the Protista, Metaphyta, and Metazoa is outside the scope of this paper.

Some implications for phylogeny. The foregoing discussion of sexual mechanisms in Monera and Protista leads us logically to a consideration of certain things for which future workers should look in the modern living world in order

[8] Possibly two kinds of crossing-over occur in the groups with protistan-type chromosomes. The phenomenon of reconstitution of wild-types in pseudoallelism has been likened to the formation of recombinant bacterial transforming principles (Ephrussi-Taylor, 1951). Recent work by Mitchell (1955) on anomalous recombinations in *Neurospora* might well be explained by a similar mechanism (*i.e.*, by crossing-over of bacteriophage type).

to test the hypotheses proposed. It is certainly true that even the most primitive surviving organisms known are entities of great specialization and perfection by comparison with what the earliest living systems must have been. Nevertheless, this should not blind us to the possibility that as yet undected organisms exist that preserve more primitive features than do any known forms. Moreover, there is much to be sought even among living groups that may put our knowledge of sexuality and thus, inevitably I feel, of early phylogeny on a sounder basis of understanding.

Of surviving organisms reproducing free in nature, those showing the simplest structure are the "pleuropneumonia-group" of organisms, which are of the same dimensions as certain of the larger viruses. Some of these have relatively simple nutritional needs (Edward, 1954). Even if, as seems not unlikely, they are degenerate bacteria (for they resemble the so-called L-forms of known bacteria), they might nevertheless recapitulate an earlier stage in moneran phylogeny. Knowledge of their nuclear processes and possible sexual mechanisms is therefore greatly needed.

The possession of chlorophyll and carotenoid pigments in certain monerans and in the simplest flagellate protists (Strain, 1951) suggests that these are a common heritage from premoneran organisms. It is possible to imagine that photosynthesis was a necessary attribute of those Premonera that gave rise to the Monera and Protista and that it has been secondarily lost in the majority of the known Schizophyta [9] and retained in most of the Cyanophyta (blue-green algae) and the myxobacteria.[10] If this is so, then one can reasonably search for photosynthetic organisms of the structural grade exhibited by the pleuropenumonia-group; in this connection the photosynthetic bacteria and even the blue-green algae should be studied for the production of L-forms.

As regards the Cyanophyta, we are greatly in need of studies designed to detect possible sexual mechanisms akin to those of *E. coli*. Some of the blue-green algae lend themselves to relatively easy cultivation (Kratz and Myers, 1955), and the way seems to be opening for studying their nuclear structure more closely and for investigating their genetics. The riddle of how the moneran groups are interrelated could be importantly illuminated by knowledge of this sort. At present the Monera, as a group, appear to be unified by such common features as a primitive sort of nucleus (which has been particularly well demonstrated recently for the blue-green algae by Cassel and Hutchinson, 1954) and possibly by the common possession of α, ε-diaminopimelic acid as a structural part of certain proteins of most monerans, but of no other organisms (Work and Dewey, 1953). On the other hand, certain important structural and biochemical differences appear to separate the schizophyte and the cyanophyte lines, although these may be more seeming than real. Thus, such of the former as are motile have "flagella" of a primitive sort, the structure of which is akin to that of the keratin-myosin-epidermin-fibrinogen group of fibrous proteins (Astbury and Saha, 1953). The latter, however (including the myxobacteria), lack vibratory organelles and characteristically move by a cellular phenomenon called "creeping motility" (see Pringsheim, 1949).

[9] A division (phylum) term for the bacteria (excluding the myxobacteria) coördinate with the algal divisions of Smith (1955) is desirable. I know that Schizomycophyta is used by some workers and that, as proposed and still used (*e.g.*, by Bergey *et al.*, 1948), Schizophyta is coextensive with Monera (the latter term being here accepted in the sense that Stanier and van Niel, 1941, used it—*i.e.*, to designate a major grouping above phylum in the living world). I am here limiting the term Schizophyta to the eubacteria, actinomycetes, and spirochetes, realizing that this is an innovation, but feeling justified because of the advantage of thus having this short euphonious name (and especially its cognate vernacular word—schizophyte) for use here.

[10] A division (phylum) name for these organisms has not been suggested to my knowledge. Such is perhaps needed, but is not appropriately to be proposed here.

The relationship of the Protista with the Monera is still very imperfectly understood. It is tempting to assume that the protistan flagellum arose by an organization of bacterial flagella into a more complex organelle. However, against this is the fact that bacterial flagella and the fibers of the protistan flagellum appear, on preliminary evidence, to be quite unrelated in chemical composition (Astbury and Saha, 1953), and there may thus be no grounds on their account for assuming a close relationship between the schizophytes and primitive protists.

Certain other characters of primitive organisms are difficult to reconcile with a phylogeny that would treat the Protista as more closely allied to the Schizophyta than to the Cyanophyta. Chlorophylls that participate in a photosynthetic system in which molecular oxygen is evolved are shared by the cyanophytes (wherein chlorophyll *a* is the only chlorophyll) and primitive protists (wherein it is in company with one other chlorophyll), whereas bacteriochlorophyll, which is never a component of an oxygen-producing biochemical system, is alone found in the photosynthetic bacteria.[11] Possibly there were many chlorophylls in the primitive premonerans, and certain ones only were retained by certain evolutionary lines. Thus the common possession of chlorophyll *a* would not necessarily indicate anything more than a remote relationship between the cyanophytes and protists. Yet bacteriochlorophyll could well be an earlier pigment in evolution since it functions in an anaërobic environment, such as is conceived to have existed before the production of an oxygen-rich atmosphere, presumably by green plant-type photosynthesis (Urey, 1952). If the earlier premonerans had the bacteriochlorophyll-type of photosynthesis and later gave rise to the green-plant type, either such occurred independently in a line leading to the cyanophytes and in another leading to the protists, or it occurred in a stock ancestral to both of these groups.

A common ancestry of the cyanophytes and protists after the schizophytes split off could explain an important enigma. The Rhodophyta, or red algae, share with the blue-green algae certain phycobilin pigments, which are otherwise unknown in the plant world. Like the blue-greens, their cells, even their gametes, have no vibratory organelles to effect locomotion. Yet the rhodophytes have highly evolved nuclei of protistan type and elaborate sexual mechanisms (see Smith, 1955; Papenfuss, 1955). It is tempting to derive the red from the blue-green algae; yet, if the Protista proper are only remotely related to the latter, then such a phylogeny demands the independent evolution of the protistan type nucleus from the moneran or premoneran level of organization in two separate lines. This is hard for me to accept.

The difficulty is resolved, however, if one assumes that actually there was a very early split in the Monera, one line leading to the schizophytes and the other to the cyanophytes and protists, including the rhodophytes; this latter line was characterized primitively by the possession of chlorophyll *a* and the phycobilin pigments. An early split gave rise to (1) the blue-green line, in which a primitive nucleus was retained and chlorophyll *a* was preserved, but not added to, and (2) a protistan line, in which additional chlorophylls were variously evolved and a higher type of nuclear organization developed. In this latter line, the rhodophytes split off early, before the evolution of the protistan flagellum; they evolved chlorophyll *d* and retained phycobilin pigments (although changing them somewhat). Another line developed the protistan flagellum, the basic fibrillar structure of which, so far as is known, shows a remarkable uniformity throughout the protistan world (Pitelka and Schooley, 1955) and is preserved in higher plants and animals—in the flagellated

[11] Recent studies (Goodwin, 1955) appear to show that the green sulfur bacteria (genus *Chlorobium*) have another type of chlorophyll, different from both bacteriochlorophyll and chlorophyll *a*.

gametes of ferns, in the cilia of metazoans and tails of their typical spermatozoa, etc. The primitive flagellate line lost the phycobilin pigments. Then it split into the "brown" line, which added chlorophyll *c* (converted to chlorophyll *e* in the Xanthophyceae of the Chrysophyta), and the "green" line, which added chlorophyll *b*.

The brown line evolved two major primitive groups—the Pyrrophyta (dinoflagellates and probably cryptomonads) and the Chrysophyta (chrysomonads, xanthophyceans, and diatoms). The latter is probably a very important basic group. From it almost certainly arose the Phaeophyta (brown algae), most of the "animal-like" flagellates, most of the rhizopods, and the Porifera (sponges). Possibly the Eumycophyta (fungi) and Metazoa [12] also arose from them.

The green line likewise evolved two major primitive groups—the Euglenophyta (euglenoids) and Chlorophyta (green algae). The chlorophytes, like the chrysophytes, appear to be a very important basic group, for from them the higher green plants almost certainly descended.

Some of the foregoing phylogenetic speculation must be regarded as highly tentative, but I hope it will help stimulate the sort of fundamental research that is needed to give substance to our understanding of primitive phylogeny. A careful study of nuclear processes, including sexual ones, may well throw considerable light on the problems involved. It must be admitted that in the Cyanophyta sexual processes are unknown and that in the Pyrrophyta, Chrysophyta, and Euglenophyta cases of sexuality are rare or doubtful on present evidence. In connection with these protistan groups, however, it seems to me more than likely that the same considerations apply to them as to the Schizophyta—rapid generation times have subordinated sexual mechanisms. Moreover, I believe that, when properly sought, such mechanisms will be found in most, probably all, primitive groups, including the blue-green algae.

It may be that the points of biochemical and morphological evidence here used to suggest certain phylogenetic connections will prove to involve much that is of independent metatropic origin—hence convergent. Moreover, when the nuclei of the Monera, both schizophyte and cyanophyte, are better understood and it is possible to recognize certain unifying features, the apparent difference between moneran mitosis and meiosis on the one hand and protistan mitosis and meiosis on the other will be breached. On these problems there is much to be done, and fascinating vistas of knowledge, now only dimly seen, will surely be unveiled.

Summary and Conclusion

In this paper the new word *metatropology* is created for the "study of organic evolution." The problem of the origin of sexuality is treated as a problem in *comparative* metatropology.

As is generally known, all modern forms of life have desoxyribosenucleic acid (DNA) in cellular compartments as a common feature. (Even the ribosenucleic acid (RNA) viruses must grow in the presence of host DNA.) I hold that sexuality, defined in terms of the regularized transfer of hereditary DNA from one cellular compartment to another, fol-

[12] Hutner (1955, p. 13) is highly tentative in making this suggestion, which gains part of its support from the fact that birds, mammals, and many chrysophytes have an absolute requirement for cyanocobalamin (vitamin B_{12}) as opposed to all other protistan and all moneran groups in which a cyanocobalamin requirement exists; in these latter, certain "pseudo B_{12}'s" can replace true "B_{12}" in nutrition. Hutner states that "B_{12} requirements have not been observed in insects." This is, however, almost certainly due to the fact that almost no insects have been grown under rigid nutritional control through more than one generation. Thus Gordon (1955) was unable to demonstrate a cyanocobalamin requirement for the German cockroach *(Blatella germanica)* during the first generation grown on a defined diet, but such a requirement *promptly appeared* during the second generation. Therefore, it appears that all adequately investigated metazoans require cyanocobalamin and that, as with some chrysophytes, no related substance can replace it.

lowed by establishment of new combinations of DNA molecules, or aggregates thereof, may be considered to be a common property of most, probably all, living groups and to provide the basis for conceiving of all modern sexual mechanisms as deriving by evolution from primitive sexuality in a "premoneran" ancestor, common to all organisms extant today.

The first sexual organism, as proposed here, was a small cellular sac containing a population of DNA molecules, which were able by one means or another to pass more or less regularly from one such sac to another, effecting new combinations in newly invaded cellular compartments. Theoretical models are here proposed for the origin of such primitive sexuality; and the evolution, from this condition, of sexual mechanisms in the Monera and Protista, and, through the latter, in the Metaphyta and Metazoa has been traced in broad outline. In so doing, I have drawn heavily upon the recently achieved and rapidly expanding picture of sexuality in the bacteria and their viruses, which, I believe, provides modern clues for the primitive sexual state.

Some general features of early phylogeny are considered, bearing especially on the relationships between the monerans and protists. I make the tentative suggestion that the Cyanophyta (blue-green algae) and Protista (including the Rhodophyta, or red algae) had a common ancestry after the Schizophyta (true bacteria) split off.

In conclusion, I should like to make the following observation: many workers have held that most microörganisms appear to have "closed" genetic systems; it seems to me a reasonable and challenging proposal to suggest in reply, "There is no such thing as a closed genetic system in the contemporary living world."

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(Concluded on p. 190)

Pogonophora

Three articles by A. V. IVANOV,
published in DAN, USSR, *vol.* 100 (1955)
and translated from the Russian by
ALEXANDER PETRUNKEVITCH

Introductory remarks by the translator. Ivanov's first paper on "New Pogonophora from Far Eastern Seas" was published in Russian in 1952. A translation of it, with omission of 12 pages of diagnoses of species, was published in SYSTEMATIC ZOOLOGY, vol. 3, 1954. That paper gave only an account of the external morphology of these interesting animals and general considerations of their relationship to other animals, as well as their division into four families. The three articles given here in a complete translation deal with the internal anatomy, external digestion and systematic status of the Class Pogonophora. At first, to avoid repetition, the translator intended to give a condensed digest of the articles. But on serious consideration, on the advice of colleagues and with the consent of the Editor of SYSTEMATIC ZOOLOGY, the decision was reached to print a complete translation in order to avoid a possible suspicion of either casual or intentional omission of material relevant to a proper evaluation of the author's conclusions, and therefore to pertinent criticism on the part of anyone who may disagree with them. The author had the courtesy of sending to the translator copies of his articles with some corrections in his own handwriting. These were included in the translation. Two of them are corrections of evident misprints in the last paragraph of the third paper where *central* is printed instead of ventral, as it should be, and the Russian word meaning *qualities* instead of the one meaning families. On the first page of the third paper Ivanov added the word *these* in the first line of the last paragraph, to make it clear that he refers to the body of Brachiata and not of all lower Deuterostomia. The translator took it on himself to change the lettering in all three figures to make it uniform. The meaning of the second sentence in the penultimate paragraph on the first page of the first paper is obscure in Russian, although from the point of view of grammar it is clearly expressed. It remains obscure in the English translation as it is difficult to understand how tubiparous glands situated in coeloms devoid of coelomoducts can secrete an external tube. The author does not mention any ducts or pores through which the secretion of the glands can reach the outside.

The second paper dealing with external digestion is not based on experimentation. One can easily understand the reason for this when one recollects where and at what great depth the animals were collected. But the conclusions based on established morphological data are so clear and convincing that no other explanation seems possible.

Ingestion of microscopical particles of food by ectodermal epithelial cells comparable to similar ingestion by endodermal cells which envelop particles by the aid of protoplasmic processes, as in Gasteropoda and various other invertebrates, is not feasible as long as there is no evidence to show that Pogonophora possess triturating organs of any kind.

Ivanov's conclusions concerning the status of Pogonophora in the system of classification are based on good evidence. Their internal anatomy has much in common with Hemichorda and nothing, except their external appearance, to show any close relationship to Polychaeta. The author proposes for the Class Pogonophora a new Phylum Brachiata, which in absence of further evidence to the contrary seems to be more reasonable than placing them as a class in any of the known phyla.

The following three articles appeared on pages 175–177, 381–383, and 595–596, respectively, in the above-mentioned volume.

The Main Features of the Organization of Pogonophora

THE Class Pogonophora (8) described in 1937 remains up to the present one of the least studied groups of the animal kingdom. Even the external morphology of Pogonophora was fully described only in 1952 (5). We find information concerning the internal structure of Pogonophora only in the works of Caullery (2, 3) and Johansson (9). However, their data require considerable additions and corrections and give no complete presentation of the general plan of structure of this group.

I have at present at my disposal already considerable material of Pogonophora, which was collected by the expeditions of the Institute of Oceanology AN USSR in the northwestern regions of the Pacific ocean. This material contains 12 species belonging to 8 genera and 4 families, already described in part.

Pogonophora are marine wormlike animals leading a sedentary type of life. They live in long, cylindrical, protective tubes, the organic substance of which they themselves secrete and which they never leave. The majority of species are restricted to abyssal depths.

The body of Pogonophora consists of a short anterior section (Fig. 1*a*) provided with a dorsal cephalic lobe (*ce*) and bearing a more or less complicated tentacular apparatus (*b*), and an extremely elongated trunk section (*p*). The latter is provided with numerous adhesive organs which exhibit in part secondary metameric arrangement. I gave a detailed description of the external anatomy in 1952 (5).

Only three segments enter into the composition of the body of Pogonophora. The first two of them are not externally delimited, but there is always present a clear circular groove (Fig. 1*s*) between the second and the third or trunk segment. Thus the anterior section of the body is formed by the two anterior segments.

The first segment forms the anterior portion of the anterior section of the body and has a single sac-like or horseshoe-shaped coelom (*coe I*) which opens to the outside by a pair of coelomoducts (*cd*). The coelomic canals of the tentacles (*coe*) are its outgrowths and consequently the tentacular apparatus represents a derivative of the first segment. The dorsal cephalic lobe also belongs to this segment.

The next segment forms the major portion of the anterior section of the body. Its paired coeloms (*coe II*) lack coelomoducts and contain numerous multicellular tubiparous glands.

The third segment is separated from the preceding one by a transverse muscular diaphragm and forms the entire extremely elongated trunk section of the body. It contains a pair of coelomic sacs (*coe III*) in which a pair of gonads are situated. The well developed coelomoducts of this segment perform the function of gonoducts (*sd*).

This interpretation of the segmentation of Pogonophora differs essentially from Johansson's scheme (9). According to him the first pair of coelomoducts in *Lamellisabella* is represented by thin-walled sacs within which the kidneys are situated. Besides, Johansson interprets the horseshoe-shaped coelomic cavity at the base of the tentacles and the coelomic canals of the latter as derivatives of the second coeloms. In reality, however, the thin-walled sacs which contain the excretory sections of the coelomoducts and which are present only in some Pogonophora represent only invaginations of the wall of the dorsal blood vessel which envelops in this manner the excretory organs, in consequence of which there is

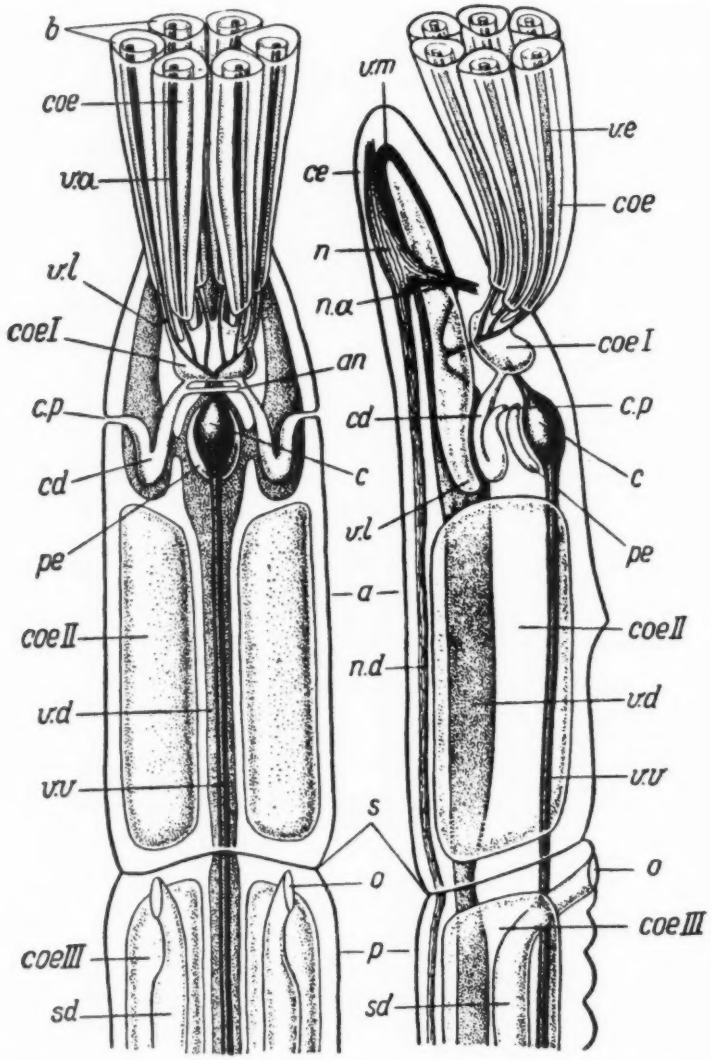

FIG. 1. Diagram of internal structure of Pogonophora. *Left,* Anterior portion of body of male, viewed from ventral side. In the tentacles only the afferent vessels are shown. *Right,* Same portion of body of male, viewed from the right side.

produced a physiological contact between the latter and the circulatory system.

The integument of Pogonophora consists of a single layer of epithelial cells, is rich in unicellular glands and is almost entirely covered by a cuticle. The adhesive structures—the bridles of the anterior section of the body, the chitinoid platelets of the trunk section and those of the belts are local thickenings of the cuticle. Mo-

KEY TO SYMBOLS IN FIGURES 1–3

a—anterior section of body
an—anastomosis of coelomic ducts
b—tentacles
c—heart
c.c—ciliated cell
c.d—coelomic duct
c.e—cephalic lobe
c.g—glandular cell
coe—coelom
coe I—coelom of first segment
coe II—coelom of second segment
coe III—coelome of third segment
c.p—external pore of coelomic duct
cu—cuticle
ep—epithelium
m—layer of longitudinal muscle fibers
n—brain
na—lateral nerve arc
n.d—dorsal nerve trunk
n.t—tentacular nerve
nu—nucleus of a pinnula
o—male genital opening
p—anterior end of trunk section
pe—pericardium
pi—pinnula
s—sulcus between anterior and trunk section
s.c—ciliated groove
s.d—seminal duct
v.a—afferent tentacular vessel
v.d—dorsal vessel
v.e—efferent tentacular vessel
v.l—lateral cephalic vessel
v.m—median cephalic vessel
v.p.a—afferent pinnular vessel
v.p.e—efferent pinnular vessel
v.v—ventral vessel.

tile epithelium is represented only by longitudinal rows of ciliated cells on the tentacles and by the broad ciliated band on the back of the anterior portion of the trunk section.

The nervous system is extremely primitive. Histologically it resembles that of Enteropneusta and is completely imbedded in the thick wall of the epidermis. One can distinguish an accumulation of ganglionic cells in the dorsal cephalic lobe—the brain (Fig. 1*n*) and arising from it the dorsal nerve (*nd*) and the lateral arcs (*na*) giving off tentacular nerves.

The closed circulatory system consists of a ventral vessel (Fig. 1 *v.v*) in which the blood flows from behind forwards, and a dorsal vessel (*v.d*) with the reverse flow of blood. The ventral vessel is provided with a muscular heart (*c*) at the base of the tentacles, the contractions of which propel the blood into the afferent tentacular vessels (*v.a*). In some Pogonophora (*Siboglinum, Oligobrachia*) there is a sac-like pericardium (*pe*) apposed to the heart on its dorsal side, probably homologous to that of Hemichorda.

The blood enters the dorsal vessel from the efferent tentacular vessels (*v.e*). Three blind branches are given off at its anterior end, directed forward into the cephalic lobe and supplying the brain with blood (*v.l, v.m*). In females the longitudinal vessels of the paired ovaries arise from the dorsal vessel behind the muscular diaphragm. In the posterior half of the trunk section the dorsal and ventral vessels are connected by numerous, branched, transverse branches.

The coelomoducts of the first segment are the organs of excretion (Fig. 1 *cd*), consisting of a ciliated canal connected with the anterior coelom, a more or less elongated and coiled excretory canal and an efferent duct. The ciliated canals of both coelomoducts are connected with each other by a transverse duct (*an*). All Pogonophora may be divided into two groups depending upon the degree of development and localization of the coelomoducts of the first segment. In the one group (*Siboglinum, Oligobrachia, Birsteinia*) the excretory sections are widely separated and are apposed to the posterior portion of the lateral cephalic vessels; in the other group (*Polybrachia, Heptabrachia, Lamellisabella, Spirobrachia*) they are long, coiled, medially approximated, apposed to the dorsal vessel, deeply bulging into its ventral wall. The first group differs besides by the presence of a pericardium which is lacking in the second group.

Pogonophora have separate sexes. Characteristic is the presence of a single pair

of greatly elongated gonads which are enclosed in the coelom of the trunk segment. The gonads are separated from the coelom by their own cellular walls. In males the testes occupy the entire posterior half of the trunk. Anteriorly they communicate with very long ciliated glandular sperm ducts (Fig. 1 *sd*) which extend to the anterior limit of the trunk segment where they open by ventral apertures (*o*). Numerous flattened, membranous spermatophores with a very long and thin filament are formed within them (5). In females the ovaries occupy the anterior half of the trunk and communicate posteriorly with relatively short oviducts. The female genital openings are situated in the middle portion of the trunk section. The eggs are fairly large, rich in yolk. Segmentation, embryonic development and the larva are not known.

The most amazing feature of the organization of Pogonophora is the lack of a gut, mouth and anus. This was already observed by Caullery (2, 3) and Johansson (9). The question concerning nutrition of Pogonophora deserves special treatment.

On External Digestion in Pogonophora

AS MAY be seen from the preceding paper (6) Pogonophora lack a digestive canal; they also lack a mouth and an anus. Naturally this extraordinary peculiarity of their structure is secondary. Their ancestors undoubtedly possessed a gut and their still unknown, free swimming larvae, the existence of which is very probable, presumably have a well developed gut.

The need of Pogonophora for continuous nourishment must undoubtedly be very great. This is indicated by their extremely high sexual productivity, by the accumulation of a large quantity of yolk in the eggs, by the intense secretory activity of the numerous multicellular glands which produce the organic substance of the very long and usually thick-walled protective tube, as well as by the fact that the growth of the animals, in particular the growth of new tentacles, often does not cease even after sexual maturity.

The key to the solution of the problem as to the way in which these sedentary denizens of the sea bottom nourish themselves while completely lacking the usual digestive system, is furnished by the analysis of their tentacular apparatus. The structure of the latter varies greatly in different species while the rest of their organization is distinguished by great constancy. The tentacular apparatus has been affected more than any other organ system in the evolution of Pogonophora. It presents a series of important systematic characters by the use of which I was enabled to distinguish four families within the limits of the class and to describe several new genera (5).

The number of tentacles fluctuates greatly: *Siboglinum* has only 1 tentacle; *Oligobrachia* 6; *Heptabrachia* 7; *Birsteinia* 12; different species of *Polybrachia* 18–70; *Lamellisabella* 28–30; *Spirobrachia* ca. 220. Judging by a series of characters, the most primitive genera (*Heptobrachia* and *Oligobrachia*) possess a small number of tentacles. The single tentacle of *Siboglinum* is undoubtedly the result of secondary oligomerization.

In all species, with the exception of *Siboglinum*, the tentacles are so placed that by being in contact with each other they enclose an intertentacular space. In *Lamellisabella* and *Spirobrachia* the tentacles even grow together. In the first genus a hollow cylinder is thus formed. In the second genus a tentacular plate is produced, which is spirally wound like a roll of paper (5).

Thus the presence of either a temporary or a permanent intertentacular cavity, of one configuration or another, is very characteristic. One may even ob-

serve such a cavity in *Siboglinum,* for in living individuals it is produced by a corkscrew coiling of the single, but extremely long, tentacle.

The structure of the tentacles in all Pogonophora is more or less the same (Figs. 2 and 3). Each tentacle is a long outgrowth of the body wall and contains a coelomic canal (*coe*) communicating with the coelom of the first segment (6). On the inner surface of the tentacles rows of pinnules are situated (*pi*) which are long and very thin outgrowths. Each pinnule represents a single very elongated epithelial cell of the tentacle, contains a single nucleus (*nu*) and is penetrated by two parallel, very fine blood vessels which unite at the tip of the pinnula; one of them is an afferent (*v.p.a.*), the other an efferent (*v.p.e.*) vessel. Penetrating the thickness of the tentacular epithelium these vessels communicate with the vessels of the tentacles themselves (Fig. 3 *v.a.* and *v.e.*). At the base of the pinnules longitudinal rows of ciliated cells are situated (*cc*). When adjoining tentacles are in contact, these rows form temporary longitudinal ciliated grooves (in the ma-

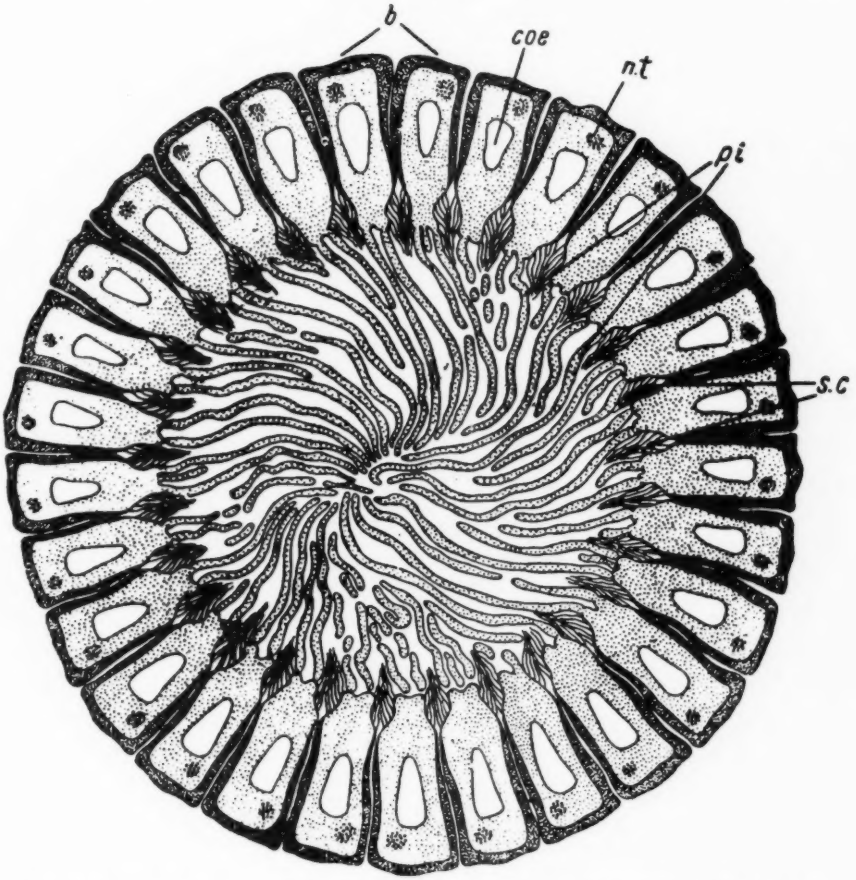

FIG. 2. Transverse section through the tentacular crown of *Lamellisabella zachsi.*

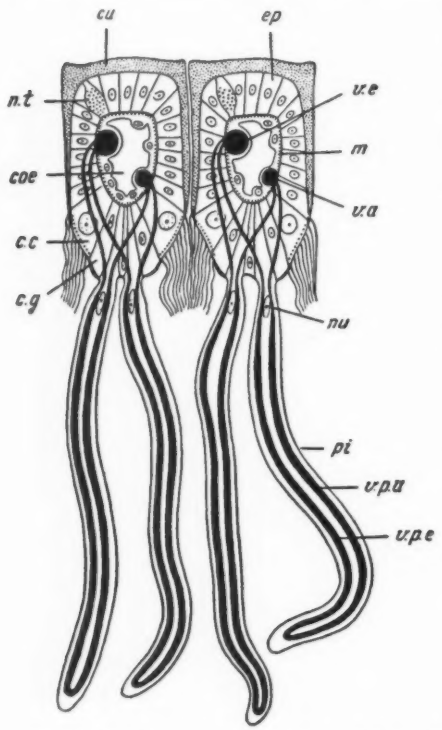

Fig. 3. Transverse section through two adjoining tentacles of *Lamellisbella zachsi*.

jority of species); when the tentacles are grown together (*Lamellisabella, Spirobrachia*)—permanent ciliated grooves (Fig. 2 *s.c.*). Rows of glandular cells are situated between the base of the pinnules and the ciliated cells (Fig. 3 *cd*). It is characteristic of all species that the pinnules face the intertentacular space in which they form a dense mass. (Fig. 2 *pi*).

One of the functions of the tentacular apparatus is undoubtedly respiration. However, we do not meet in a single aquatic animal with such a fine, really microscopically fine subdivision of the respiratory organs, nor with such a perfect supply of blood within them. Apparently neither the pinnules themselves, still less the intracellular vessels within them, are necessary for gaseous exchange which may be accomplished without such adaptations. It is evident that the tentacular apparatus has still some other important function besides respiration.

All these facts and considerations persuaded me that the tentacular apparatus serves for collection of food, its digestion and resorption of its products.

Being immobile sedentary animals, Pogonophora can have only a passive type of nourishment, that of filterers or collectors of plankton and detritus. It is probable that the beating of the ciliated grooves of the tentacles propels water into the intertentacular space, into which it enters through the opening at the distal end of the crown and which it leaves through an opening at the base of the ventral tentacles, an opening which is always present even in species with fused tentacles. Microscopic organisms and detritus suspended in the water are caught by the dense network of the pinnules, which thus plays the role of a filter. Digestive enzymes are secreted into the intertentacular space probably by the above mentioned glandular cells. Here digestion of the food takes place. The nutritive substances are resorbed by the pinnules which play the role of peculiar "intestinal villi," and pass into the blood of their vessels from where they reach the dorsal vessel with the blood flow from the efferent tentacular vessels and are distributed throughout the body. It is possible that the filtration of water by the tentacular apparatus and the digestion of the food do not take place at the same time, that is, that first a certain reserve of food is accumulated and that then the animal digests it after having withdrawn the crown of tentacles into the tube.

Pogonophora represent therefore a unique example of free-living (non-parasitic) animals lacking a digestive tract and possessing exclusively external digestion.

On the Assignment of the Class Pogonophora to a Separate Phylum of Deuterostomia—Brachiata A. Ivanov, Phyl. Nov.

JOHANSSON (9), having recognized that *Lamellisabella* belongs to a special class Pogonophora, has placed it close to the Phoronidea. However, the trunk of the latter represents a greatly extended ventral outgrowth of the larva and does not correspond to the trunk of the Pogonophora. Besides this, Phoronidea possess only two pairs of coeloms, gonads not separated from the coelom, and a pair of lateral nerve trunks.

Much nearer to the truth is the opinion of Dawydoff (4) and Beklemishev (1) who place the Pogonophora near the Hemichorda. Now, when the organization of the Pogonophora is clear in its main traits, one can point out a series of characters in common with the Hemichorda. Such are: the composition of the body of three segments, the single anterior coelom, the pericardium, the coelomoducts of the first segment, the situation of the gonads in the trunk segment and their separation from the coelom, the dorsal nerve trunk and the epithelial position of the nervous system. Besides this, a peculiarity in common with the Enteropneusta is the secondary metamerization of the elongated trunk section, although in Pogonophora secondary metamerization affects also other organs.

Notwithstanding this it would be wrong to include Pogonophora as a subphylum in the Phylum Hemichorda, as is done by Beklemishev (1). This is contradicted by the belonging of the tentacles to the first and not to the second segment as in Pterobranchia, by the strong development of the anterior coelomoducts which have an excretory function, by the absence of these organs in the second segment and by their development in the trunk section. Among the distinctive characters of Pogonophora are: the development of the brain in the first and not in the second segment, the development of the heart from the ventral and not from the dorsal vessel, and finally the strong cuticularization of the integument. The absence of gill slits and of a notochord cannot serve as distinctive characters because of the secondary reduction of the digestive tract.

A series of peculiarities of the organization of Pogonophora developed under the influence of sedentary life. To these belong: the ability to secrete a protective tube, the extraordinary length of the trunk and the substitution of the digestive tract by a peculiar tentacular apparatus which performs the functions of accumulating, digesting and resorbing the food (7).

All this forces us to regard the Pogonophora as an independent phylum of Deuterostomia which I propose to call Brachiata.

The Phylum Brachiata may be characterized as follows. The body of these lower Deuterostomia consists of three segments of which the two anterior ones form by fusion the anterior section of the body. The first segment contains a single coelom with a pair of excretory coelomoducts, and forms the dorsal cephalic lobe and the tentacular apparatus. The second segment is without coelomoducts. The trunk segment is greatly elongated and contains a single pair of gonads; its coelomoducts function as gonoducts. The integument is cuticularized; ciliated epithelium is retained only partially. The brain belongs to the anterior segment; from it the dorsal nerve trunk originates. The entire nervous system occupies an epithelial position. The circulatory system consists of a dorsal and a ventral vessel connected anteriorly by a system of vessels of the tentacular apparatus. There is a muscular ventral heart which some-

times is supplied with a pericardial sac. The sexes are separate. The gonads have their own walls. The testes lie in the posterior, the ovaries in the anterior half of the trunk segment. The spermatozoa are enclosed in membranous spermatophores. Segmentation and larva are not known.

A single Class Pogonophora Johansson, 1937, belongs to Brachiata.

In a previous communication (6) I have already presented the reasons for dividing the Class Pogonophora into two orders. Their brief characterization is as follows:

1. Order Athecanephria A. Ivanov, order nov. Anterior coelom sac-like. Excretory sections of coelomoducts of first segment widely separated and apposed to the surface of the lateral cephalic vessels. Heart supplied with a pericardium. Family Siboglinidae.

2. Order Thecanephria A. Ivanov, order nov. Anterior coelom horseshoe shaped. Excretory sections of coelomoducts medially approximated, greatly convoluted and situated in the ventral sac-like invagination of the wall of the dorsal vessel. Pericardium lacking. Families Polybrachiidae, Lamellisabellidae and Spirobrachiidae.

REFERENCES

(Translator's note: In the original, references are given at the end of each of the above articles. To avoid repetition and confusion, they are all given here and the parenthetical numbers referring to the listed references have been changed accordingly.)

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The work of Dr. Pierre Bonnet, *Bibliographia Araneorum,* the first volume of which came out in 1945, is continuing. The first part of volume II has recently appeared, and contains 918 pages. Those interested in obtaining copies may write to Dr. Bonnet himself, at the Faculté des Sciences, Université de Toulouse, France. The price is $23.00.

Terminology of Microgeographic Races in Mammals

J. KENNETH DOUTT

ONE of the basic functions of language is that of giving names to objects. If we order lumber for building a house, it is important that we be able to specify whether we want oak or pine—or whether it should be white pine or yellow pine. We recognize that different species of plants and animals have different characteristics and that what is true of one may not be true of another. The common field mushroom, *Agaricus campestris,* is good to eat, but the white amanita or death angel, *Amanita verna,* is deadly poisonous. We not only need to be able to recognize different organisms, but we must have names under which we can classify our information about each one. Otherwise our observations may be applied to the wrong organism. By attributing the observation to the wrong species it may become misinformation, and thus be worse than useless. Thus it becomes obvious that having the correct name for an organism is exceedingly important.

If two organisms are different in any respect, it may be of great importance to be able to distinguish between them, even though they may be identical in appearance. Thus it is the duty of the taxonomist to discover and name the different kinds of organisms with which he works and to point out characters by which they may be recognized. On the other hand, it is the province of taxonomy to classify as well as to name, and classification is based on the principle of uniting, under one name, organisms which are related genetically.

The only thing which we can pick up, measure and examine, is the individual. All of the categories in which we classify things, such as the microgeographic race, subspecies, species, genus, etc., exist only in the mind. Yet some of these concepts are exceedingly fundamental, not only in the mind of man but in the minds of many other kinds of animals as well. This thesis will be developed a little further on, but for the moment it is necessary to stop and consider the importance and extent of individual variation within the species. If we think of people we know or have seen, we recall (without considering anomolies such as giants or dwarfs) some huge men—well over six feet—others may be scarcely more than four feet, some are thin and tiny, weighing eighty pounds or less, while other ponderous hulks may weigh over three hundred pounds. Then consider the enormous differences between a baby only a few hours old, a child of five or six, a young man of twenty and an old man of ninety or more. What enormous changes take place between birth, maturity and old age. We are often inclined to feel that other species show less variation than does the human race. However, this is largely because we are less familiar with the details of other species. I have been impressed with the extent of individual variation in each group I have studied. In the genus *Phoca* I commented on the subject as follows (Doutt, 1942, p. 99): "The genus *Phoca* is remarkable for the amount of variation which may be found among the individuals of any species. Practically all former students of the group have commented on this fact. In some instances, variation within the genus is sufficient to overlap the specific characters. Thus, a skull of one species, in some rare cases, may be so abnormal as to be mistaken for that of another species. The greatest single cause of variation within the species can probably be ascribed to age. Indi-

vidual variation, regardless of age, is extensive also."

Through all of this extensive individual variation, however, there is a similarity which makes it possible for us to recognize a specimen as belonging to a given species, and the species—not the subspecies nor the genus—but the species is the basic unit with which we deal. Interbreeding, for example, is accomplished up to the species level, but beyond this it becomes difficult or impossible. Suture closure in the skull is usually constant for the species, but differs in different species (Doutt, 1942, p. 106). This indicates a fundamental physiological similarity in the species which produces a similarity in growth and form. Although a vast amount of variation may occur within the species, it still is the natural unit with which we deal.

There has been much discussion about what constitutes a species, and taxonomists still do not agree upon a definition, yet the fundamental basis of the concept is so elemental that even a mouse has some understanding of it. It is obvious that at mating time mice have little difficulty in recognizing others of the same species. Of the many kinds of plants which grow about their habitat they seem able to distinguish between those which are good and those which are not good for food or nesting material. They recognize those species of other animals which are their enemies and those which are harmless to them. The same is true of birds, insects, and many other kinds of animals. If these so-called lower animals can distinguish between different species it would seem that the species concept should not over-tax the capacity of the human mind too severely. Our binomial system of nomenclature was devised to show the genetic relationship which is inherent in the species concept and I do not believe any thinking biologist would recommend abandoning this system at the present time. However, it is possible that improvements may be made on it and Gould (1954) has made an interesting suggestion for the use of numbers.

In species which are distributed over wide areas, where there are natural barriers to their distribution, or where the gene flow for some reason is restricted, there is a tendency for these separate populations to become distinct. When these separate populations have become recognizably different, we have customarily called them subspecies and have given them Latin names with all the nomenclatorial sanctity accorded a full species. This trinomial system of nomenclature has proven to have definite advantages in showing the relationships of the various populations of a species.

However, in mammalogy at least, and in some other branches of zoology also, there has been a recent tendency to describe as subspecies every local population which could be shown to be even slightly different. Some authors have used the "50 percent rule," believing that if they could distinguish 50 percent of the individuals, they were justified in recognizing them as belonging to a separate subspecies. Other authors have adhered to the "75 percent rule," or the "84 percent rule," or some other rule. In any case, however, only a certain portion of the population can be identified; the rest must be classified with another subspecies or be labeled as intergrades. Statistical analysis may be necessary to establish the identity of the population. This requires long series of specimens, both of the population to be identified and the populations which are being used for comparison.

If we consider the subspecies to be a fixed unit, this approach might seem justifiable. Recent studies, however, have indicated that most microgeographic races are not fixed units, but are small local segregations which are in a constant state of flux.

A more complete knowledge of the nature of these local populations—or microgeographic races—has cast grave doubt on the advisability of naming them as subspecies and granting them recognition in our formal system of nomenclature. If they fluctuate from place to place and from time to time as rapidly as is indi-

cated by recent studies, they certainly do not deserve formal recognition. Much of our trouble with subspecies in recent years has been caused by our failure to distinguish between these two categories, i.e., the subspecies and the microgeographic race. If we could eliminate from our check lists all those names which apply only to microgeographic races, I believe our system would not only be simplified, but would also be much more intelligible. The characters which separate these local populations are of a considerably lower order than are those which separate different species. In the full species, the characters are usually firmly established and easily recognizable. In the microgeographic race most of these characters are not easily recognized and are not firmly established, but are subject to constant change. The subspecies lies somewhere between these two extremes, and in a well-defined subspecies, some characters may be fairly well established. The differences which exist between species, subspecies and microgeographic races are ones of degree, and it is difficult to know just where to draw the line. If this problem can ever be resolved it will require much further study and I shall not attempt to define the limits now. In most instances, however, I think subspecies should be based on characters which remain relatively constant in the population for some period of time. If possible, they should also be phenotypic characters which can be observed easily in the kind of material which is customarily preserved for study. If we recognize as a subspecies every local population which can be shown to be recognizable, we will eventually have to name as subspecies the mice from every valley and every mountainside—perhaps even from every woodlot! This same attitude toward local populations was very ably stated by Mayr, Linsley and Usinger (1953, p. 33):

> The subspecies is the lowest taxonomic category which it is advisable to distinguish nomenclaturally. However, the subspecies is by no means the lowest subdivision of the species. Subspecies are not homogeneous but are composed of numerous local populations, all of them differing slightly in gene frequencies and the mean values of various quantitative characters. . . .
>
> Now that it is being realized that every local population is different from every other one, even if they live only a few miles apart or less, and that these populations are not sharply separated from one another (except where separated by unsuitable areas), there is no longer a valid excuse for the formal nomenclatural recognition of innumerable local subdivisions of subspecies. It is legitimate and even desirable to describe the trends of variation within a subspecies—particularly if material from numerous localities is available—but it serves no useful purpose and merely complicates nomenclature to give names to these localized, slightly different populations or colonies.

In 1946 Carnegie Museum enlisted the cooperation of the Pennsylvania Game Commission and the U. S. Fish and Wildlife Service in a study of the mammals of Pennsylvania. With the aid of Pittman-Robertson funds we were able to make a comprehensive study of the entire state. During the next six years approximately 15,000 specimens of mammals were collected in the state. Over the years, Carnegie Museum had assembled about 5,000 specimens, so the mammalian fauna of Pennsylvania is now represented at Carnegie Museum by approximately 20,000 specimens. Some species, such as *Microtus pennsylvanicus* and *Blarina brevicauda* are represented by several thousand specimens.

With this wealth of material at hand I asked Mr. John E. Guilday to make an analysis of the variation in local populations of *Blarina,* and Dr. Dana P. Snyder to make a similar study of *Microtus.* The results of these two studies are being published separately in the Annals of Carnegie Museum.[1]

In both studies the characters used were ones commonly employed to distinguish subspecies in these groups. Although standard characters were used, it has been possible to show that there is as much difference between certain colonies, only a few miles apart, as there is be-

[1] Guilday's paper is ready for publication and will appear shortly.

tween other groups which have been described as subspecies. Snyder (1954, p. 210) comments on this subject as follows:

It is obvious that considerable geographic variation occurs between areas which are quite near each other. Areas D, E, and F are all within a radius of 15 miles. It is also apparent that not all populations show such variation, even though they may be separated by greater distances. The variation in skull length as well as in a number of other dimensions was tested by an analysis of variance. The resulting ratios . . . show that, with the exception of cranial breadth and cranial height, variation within the area is highly significant. There is, accordingly, little reason to doubt the realty of appreciable phenotypic variation among populations within this relatively small area.

Again, on page 224 he says:

These conclusions do not indicate that large samples covering relatively large areas are not valuable for describing average characteristics of a given species or subspecies. However, they do point to the probability that the local populations are the more basic units. This corroborates what has been evident for some time, that populations differing considerably in absolute size and in proportions may occur within such a small area that formal recognition of them as geographic races or subspecies is neither practical nor desirable. Nevertheless, in studies of wider geographic scope, knowledge of these local variations is very desirable, since clinal trends may be obscured if some of the collecting localities happen to represent extreme local populations. Furthermore, the magnitude of variation between these local populations may approach that occurring between recognized subspecies thus destroying the objective basis of delimitation of these geographic races.

Further on he says (page 227):

In order to indicate the importance of variation among local populations, samples from other populations of *Microtus pennsylvanicus* in northeastern North America were measured and the means plotted. . . . As above, skull length is plotted to show variation in absolute size; the other dimensions to show variation in proportion. The samples were allocated to the following subspecies on the basis of Hall and Cockrum (1953): *pennsylvanicus* from Ontario (Peterboro, Kent, and York counties), *fontigenus* from Ontario (mouth of Moose River), and from southeastern Quebec (St. Margaret, Natashquan, and Kegashka rivers), *enixus* from Labrador (Red Bay, Battle Harbor, Windsor, Nain, and the Hamilton River), *labradorius* from Quebec (Nastapoka, Koaksoak, and Great Whale rivers). It is somewhat surprising to find that these populations are quite similar to those in Pennsylvania. Although only relatively small series have been measured, these were (as in the case of the Pennsylvania specimens) selected from a much larger number the great majority of which were immature. The samples should therefore be more representative for our purpose than a larger series containing many younger age groups. It is evident from the graph that with few exceptions the means of the samples of *fontigenus, enixus,* and *labradorius* as well as the Ontario *pennsylvanicus* are within the range of the means of the samples from Pennsylvania. The greatest deviation from the Pennsylvania material is shown by the length of diastema in the sample of *enixus,* and in this case the difference is just on the borderline of the commonly accepted level of significance.

It appears that, on the basis of the skull characters used here, samples such as these could not be properly placed with regard to subspecies without a knowledge of the geographic location of the specimens. Since these samples do not constitute topotypical material, no inferences are drawn regarding the validity of the subspecies. Furthermore, other characters could no doubt be found by which these populations could be recognized under prevailing concepts. It may be noted though that Weaver (1940) who had topotypical material of both *pennsylvanicus* and *fontigenus* did not regard the latter as a valid subspecies and referred his specimens from the southern coast of the Labrador peninsula to *pennsylvanicus*. However, the problem presented by these results is not one of finding characters to separate various forms but of arriving at a clear-cut and unambiguous basis for erecting a subspecies. It will probably always be possible to find differences between any two populations; the difficulty is in deciding when the differences are important in relation to the end in view. Perhaps it is time to re-examine the basic concepts by which we continue to describe and recognize mammalian subspecies in order to determine just what is 'the end in view.' Then we can arrive at some conclusions regarding the purposes and values of infraspecific categories—purposes and values which should benefit the phylogenist as well as the nomenclaturist.

If we were to follow the practice of many zoologists who believe that every recognizable population should be named, we would have to describe several new subspecies of *Microtus* and *Blarina* from

Pennsylvania. Such a procedure seems to me to be an unrealistic approach to this problem, and I do not believe that the fundamental purpose of taxonomy would be served to best advantage by this means. The multiplicity of subspecific names which have been given to what are actually only microgeographic races has so cluttered up our nomenclature that we have lost much of the value of our classification. Since classification is an essential part of taxonomy, it becomes important that we find some way of handling these microgeographic races, without giving them Latin names.

On April 17, 1952, I presented a paper to the American Society of Mammalogists, at their convention in Charleston, South Carolina, in which I discussed this same subject, and suggested the use of geographic terms in place of subspecific names for what are actually microgeographic races. The following paragraphs are quoted from that paper.

> It would be possible for us to handle any number of different groups by using a subspecific name which applies to a large area like northeastern United States and then applying the geographic name for the locality from which it came. For example, *Microtus p. pennsylvanicus* from New Springfield, Pennsylvania . . .
>
> The geographic term gives us immediately the specific locality from which the animal came. It makes it possible for us to handle any number of populations or groups without the need for coining new names and memorizing localities and relationships for them.
>
> . . . It makes the handling of populations infinitely flexible, yet it avoids cluttering up our literature with a multiplicity of names and it does not require the addition of any information which is not already on the label.
>
> To put it all briefly—it is possible by careful study of long series of specimens to distinguish many geographic races. But if we do recognize them it will be possible to identify a specimen only by having a long series for comparison.
>
> Would it not be better to restrict the use of subspecific names to populations which are so distinct that any individual specimen can be distinguished by easily recognizable characters? We can then use the geographic term for splitting the subspecies as fine as circumstance requires.

Further study of this problem has convinced me, even more, that the naming of local populations as subspecies is not justified.

The idea of using geographic references to designate local populations is not new. Dice and other students of mammal populations have been using such references for many years, in designating particular stocks which they have studied. The following sentence quoted from Dice (1949, p. 29) illustrates his use of the term. "It will be noted that in comparison with the other Oregon stocks previously reported, the Hood River stock more closely resembles in tail length the stock from Eugene, which lies in a somewhat open interior valley, rather than the longer-tailed stocks from Tillamook, Coos Head, or Port Oxford, all of which localities lie in the more densely forested belt along the coast." These terms are adequate to designate the populations with which he was working, yet they do not clutter up the literature with useless terminology. Furthermore, they have much more meaning to the reader. The use of geographical terms to designate local races provides a stability and universal understanding comparable with the Latin names which we apply to higher categories, because geographical terms are, for the most part, applied consistently to the same place and are universally understood.

In a recent paper Wilson and Brown admirably defend this idea. They even suggest the abandonment of the subspecies and the use, in its place, of a geographical term. I would not go so far as to suggest the abandonment of all our subspecific names, for some of them serve useful purposes (e.g., *Peromyscus maniculatus bairdii* and *P. m. nubiterrae* or *P. m. rufinus* and *P. m. sonoriensis*). These distinct subspecies have their place in our taxonomic system, but for many of the poorly defined subspecies, and all the microgeographic races, I would prefer to use geographic terms.

Mayr (1954, p. 87) has questioned the advisability of using the locality as a

designation for subspecies. In this matter I agree with him for I, too, believe that we should not substitute locality names for well-defined subspecies. However, many of the populations which have been described as subspecies are really only microgeographic races or ephemeral populations, and it is this category which I think should be removed from our taxonomic hierarchy. Names of this nature should not be permitted to clutter up our check-lists or be granted the sanction which is accorded a subspecies. It is for taxonomic categories of less than subspecific rank that I would propose the use of geographic terms.

The populations of less than subspecific rank which have already been described as subspecies should be synonomized with the subspecies to which they belong. In the future these populations should be referred to by locality or some other designation which would not involve our trinomial system.

There is some question as to how long one of these microgeographic races may remain the same. There seems to be a tendency for them to change with time as well as with space. Is a colony of *Microtus* the same this year as it was last? Will it be the same five years, ten years or twenty years from now? It seems quite possible that it will not be, and series of specimens taken at the same place several years apart may be recognizably different. I first became aware of these problems in 1939 during studies on the genus *Phoca* (Doutt, 1942, p. 116) and *Clethrionomys* (Doutt, 1941, p. 162) which I conducted more or less simultaneously. I was impressed with the degree to which *Clethrionomys* segregates into isolated local races, especially in Pennsylvania. On page 163 I commented on the subject as follows: *"Clethrionomys gapperi* is a widely distributed species in the northern part of its range, but towards the southern limit it becomes restricted to isolated bogs or mountain tops. In these latter situations it is cut off from other members of its kind. Each of these communities may develop distinctive characteristics and finally produce recognizable geographic races."

I gained the impression that *Clethrionomys* was more subject to isolation in Pennsylvania than most other genera of the Cricetidae and that these isolated groups were liable to develop into local races. At first I was inclined to describe these local races as subspecies, but before I had finished my study of the genus *Phoca* I had reached the conclusion that local races of this kind were too subject to change by swamping of characters to be worthy of recognition as subspecies. I did not describe the specimens from Boothbay Harbor, Maine, as a new race, but commented on this subject as follows:

> The great amount of variation in the genus often leads to the description of local races, when the number of specimens available is not sufficient to justify such conclusions. Also, in the genus *Phoca*, there seems to be a tendency toward the establishment of local clans; that is, a number of specimens taken at the same time show a great similarity, but other specimens taken, years later, at that same place may be quite different. It seems that the dominant characteristics of a particular strain may be established for a time at a given locality, but after a while these characteristics are swamped by others—perhaps by the introduction of new blood from other localities. For example, four specimens in the American Museum collection from Boothbay Harbor, Maine, all taken at the same time, are very similar, and are so distinct from specimens taken at other localities along the New England coast that they might be described as a new race, but I would consider such a course very inadvisable.

If we consider time in the paleontological sense, it is certainly one of the most potent factors in the development of new forms. Without the element of time no differences are produced, for it takes some time to produce even one generation of any species. Fifty million years is sufficient time to produce enormous change in some groups. Other groups, however, such as the opossums of the family Didelphidae have shown relatively little change even in sixty million years. It seems that the rate of change is different in different groups. The factors which produce the changes we see, and those which influ-

ence the rate of change are not well understood as yet, but it is certain that time is an essential element in all of them.

The amount of time required to produce detectable change in a species is a subject which needs much additional study. The isolation of *Phoca vitulina mellonae* in Seal Lake (Doutt, 1942, pp. 74–78) is an example. In this case I estimated that a new subspecies was produced in about 5,500 years, plus or minus 2,500 years. Simpson (1944, p. 19) points out that this would be about 1,000 generations. He suggests that in some rodents subspecific differentiation might take place in even less than 300 generations. These figures, it must be remembered, are for the production of a new subspecies. It is my opinion that the production of the microgeographic races which we are now discussing may be of an entirely different magnitude, and that differences may be demonstrable in a matter of only a few years.

It would seem that it might be well to use the year, as well as the locality, to designate local races, for if additional studies which are now in progress prove our assumptions to be correct, specimens taken at the same place, but in different years, may be as different as specimens taken at different localities. In other words, these microgeographic races, and many so-called subspecies, may be only shifting aggregations which are not constant either in time or place. They differ from one another by characters which are of an ephemeral nature. Such races, or groupings of individuals, have no place in our taxonomic hierarchy.

If our studies on this subject prove this assumption to be correct, it brings up the question of topotypes. How long will it be possible to collect, at the type locality, specimens which actually represent the type? Perhaps we should add to our term "topotype" a prefix indicating *when* the topotypes were taken. We could use the term "hama-topotype" [2] for specimens taken at the same time, or within a few months of the same time, as the type, and "neo-topotype" for specimens collected at the type locality, but some years later. Following the word "neo-topotype," and in parentheses, should be a figure indicating the number of years later that the "neo-topotypes" were collected.

[2] "hama"—from the Greek word meaning "at the same time."

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In Defense of the Subspecies

STEPHEN D. DURRANT

THE recent literature contains articles in which the main arguments are against the preservation of the category of the subspecies, its trinomial and its preservation under the rules of the International Commission of Zoological Nomenclature. Two papers in particular are of interest to me, because Wilson and Brown (1953, pp. 102–103), used my work as an example, and in the other Burt (1954, p. 99), referred to me by inference because by naming subspecies of *Thomomys bottae* I am responsible for approximately ten per cent of "our most horrible example" of misuse of the subspecies in mammalogy. Naturally, when my studies and their results are so diametrically opposed to the thinking of others, it is time for reevaluation and critical study of my position and philosophies. This necessitates a careful analysis of the facts and concepts on both sides of the problem.

At the outset, I might say that I am a student of animals, not categories. I care not what populations are called, or how they are discussed, providing the most meaningful system is employed. I consider the greatest worth of the subspecies to be its use as a cornerstone in the foundation of the study of evolution. It is the most important tool that students of evolution have from the viewpoint of geographic variation and distribution, in attempting to contribute to the understanding of what happens to animals at the level of the infraspecific categories. Furthermore, the use of the subspecies is not necessary or perhaps even meaningful to students of variation who have other aims in their studies.

The authors mentioned above agree that the formal subspecies should be relegated into obsolescence or even abandoned, because to them it contributes nothing to the understanding of the animals in question that cannot better be obtained by simpler, less involved means. Furthermore, they consider that the increased use of the trinomial, with its entailed synonymies and realignments, will ultimately add up to total confusion, and that it is incapable of adequately expressing the purposes for which it is currently employed. Careful reading of the above articles will inform the reader that the authors consider the major worth of the subspecies to be only that of establishing the extent, degree, and limits of geographical variation. Burt, in commenting upon the 150 subspecies of *Thomomys bottae* asked what this showed of biological importance, and commented "it shows that *Thomomys bottae* is highly variable throughout its range." To me, this is only one of the contributions of the study of subspecies and is far from the most important. Nowhere did I find criticisms directed against the use of the subspecies with reference to its values as concerns the explanation of rates, degrees and significances of variation. I agree, that for the limited usage they apparently purport to make of the study of variation, they do not require the subspecies and its trinomial nomenclature. Wilson and Brown propose as a substitute for the subspecies and its trinomial that merely the species name be retained followed by a local vernacular geographic name as a citation for the geographically varied population. Likewise, Burt would retain only the species name but would express morphological variation by means of symbolic maps. I fail to see where the employment of vernacular names for localities of occurrence of populations would simplify or adequately resolve the problem. I can readily appreciate how it could lead to far greater inaccuracies and considerably more involvement. It could not obviate

the necessity for naming populations, and offers at best a more cumbersome, less specific system than the one employing the formal subspecies. What about areas in many states, particularly in the west, where several localities bear the same vernacular name? In attempting to clarify such a situation, whole sentences would be required to replace the trinomial. Furthermore, this type of designation could contribute little toward establishing the relationships between populations, and would establish nothing of the degrees of difference. If unit characters, like color, which Burt used in his example of *Neofiber,* were being investigated and clines established, maps would be applicable in some instances. They seem to me to be inadequate if several characters were being considered simultaneously. Such a scheme should work rather well with concordant characters, but what about discordant characters? If such maps were prepared, in order to clarify the symbols on the maps, there would be of necessity considerable naming of populations, for which no adequate system is provided. All these weaknesses are mostly obviated by the use of the trinomial in the formal subspecies. Furthermore, it must be borne in mind that clines and subspecies are not synonyms, each applying to different aspects of variation.

Their criticisms are valid in part, and certainly substantiate their contentions in keeping with their concept of the study of subspecies, and their purposes in its usage. I raise the question, however, as to whether the concept of the formal subspecies is wrong, or whether it has become distasteful because of abuses. I also raise the question as to whether the criticism of the present concept of the formal subspecies, and its employment, can be equally applied to all kinds of animals in all different geographical localities. Undoubtedly the basic biological phenomena are essentially the same for any given kind of animal in any geographic area, but the tools for explaining them may be quite varied and useful under different given conditions. It is well known that the criteria that are in current usage in vertebrates for establishing even the species cannot be employed in some of the invertebrates and plants. The study of subspecies of mammals of the Great Plains region, with their extensive ranges and wide zones of integradation possibly requires a system considerably different from that required to understand the mammals in the small, discrete, isolated ranges in the intermontane west with its highly varied physiography. The formal subspecies with its trinomial has proven to be extremely satisfactory for understanding subspeciation, rates and amounts of variation, and degrees of genetic fixation in mammals from Utah. I can appreciate that in the Great Plains region, for instance, it might not be so adequate or even necessary in many cases. Because of this, are we justified in excluding the subspecies even though it is a fine tool for understanding subspeciation in mammals from Utah? A round-mouthed shovel is of little value in a rock quarry, but a pneumatic hammer is an efficient tool, so by the same token we should do away with all round-mouthed shovels. I see nothing in the substitute proposals which negate the value of the formal subspecies in the total understanding and explanation of the phylogenetic trends within the species.

Possibly the best way to analyze this problem is to consider in a more detailed manner some of the criticisms and the suggested remedies that have been set forth. Wilson and Brown enumerate their conclusions. Some merit special remark, while others need no qualification. In the second section of their summary, they state ". . . the subspecies has been defined as a genetically distinct geographical fraction of a species." In addition, they state that following certain diagnostic characters, the subspecies is a "concrete unit." These concepts have been contravened according to them. Among others, I have never supported the concept that a species is fractioned into subspecies.

Rather, my understanding is that a species is somewhat more than the sum total of its fractions. This is a different connotation than the critics entertain. What about those members in all of the populations who have not developed any recognizable, stable genotype worthy of definite subspecific status? Can these be considered by the same standards as those populations that are now distinct? In my thinking, subspecies have never been concrete units. As a matter of fact, I consider them for the most part, to be populations which have attained sufficient genetic stability to develop a recognizable phenotype only in the majority of their members. In most instances, my studies have led me to consider the majority of subspecific characters to have little adaptive worth. Then why bother with a subspecies name for animals in this unstable condition? Would it not be better as the previously mentioned authors have stated, simply to designate variation by some other method?

Now we come to the crux of the problem. If it is only desired to learn and discuss the extent and limits of variation within a given species, then this can be done without the designations of subspecies and the employment of the trinomial. If in addition, it is desired to evaluate and document the degrees of change, and the rates and amounts of genetic fixation, then it is imperative that the tools for explaining the various degrees of differentiation be provided. This is where the value of the subspecies becomes important. Certain populations which have attained sufficient genetic stability are named as formal subspecies and immediately the standards are established for meaningful comparative analyses and syntheses, not only of the amount of variation within the species, but the yet nonstable populations, and the yet non-distinctive members of otherwise stable populations can be aligned and studied with references to definite standards. This appears to me to be better bookkeeping and alignment of data. In order to evaluate any type of variation, standards of comparison must be established, and the formal subspecies is the cornerstone of these standards.

Another serious criticism of the subspecies is its arbitrary usage in polytopic races and microgeographic races. I agree that the use of the formal subspecies should not apply to polytopic races, but disagree as concerns its usage in microgeographic races. Are we studying animals or their areas of occurrence? Is it the degree of variation and distinction of the animals themselves or the size of their ranges that decide if they merit taxonomic designation? Personally, I cannot conceive of any reason why the size of a population or the size of its area of occurrence should have any significance with reference to its taxonomic status. Subspecies are named on the basis of their morphological differentiation, which bespeaks a genetic stability, and not on the size of the range. Some subspecies of pocket gophers having small (microgeographic) ranges are more distinctive morphologically than are some sympatric species in some other genera of mammals, e.g. *Citellus*. Among others, Burt deplored this naming of microgeographic races in *Thomomys bottae*, but students of these mammals know that in animals as sedentary, as edaphically restricted, and as morphologically variable as are members of this species, that this is the expected rather than the unusual situation. It is well known that genetic fixation is extremely rapid in small, isolated or semi-isolated populations. It is true, moreover, that in some kinds of mammals, many small, local populations are only demes, and are but strains in geographic distribution, but in animals such as pocket gophers and kangaroo rats in the intermontane west, this, in my judgment, is not the case. In Utah, many species of mammals attain their distributional limits, and along the margins of their ranges they have broken up into small isolated or semi-isolated populations which have undergone, and are undergoing,

rapid subspeciation. Here we see evolution at work, and when these populations attain significant genetic distinction, the designation of them as subspecies much more adequately documents their degree of change and advancement than could ever be explained by any local vernacular assignments or symbolic maps. The application of the subspecies to them puts a unified, standard mark upon their degree of variation and concisely depicts their relationships. The giving of a trinomial, with a formal description and a range of occurrence, establishes standards that are about as uniform to all workers as any study as subjective as subspeciation could hope to attain. Furthermore, I might state that the solutions offered by the critics are not novel and have been employed to no avail by myself and other workers. They do not resolve the problems as well as does the usage of the subspecies. Should we then be denied the tools that are so efficient in our studies, because they do not apply to all kinds of organisms in all geographic localities?

Another criticism of the subspecies is the difficulty of establishing its lower limits. This is real and is probably where the bulk of the abuses occur. Perhaps with the exception of the species, which appears to be the most natural taxonomic category by reason of reproductive isolation, the same criticisms could be leveled at many of the other taxonomic categories. Is there real unanimity of opinion on the lower limits of some phyla even? The decisions on limits are all rather subjective, and will never be any better than the judgment of the persons who make them. Naturally, the closer the approach to the lower taxonomic categories, the greater the possibility for error. But should this be sufficient reason for abandoning the subspecies? In the hands of a competent, careful student, the subspecies can be of real worth in the advancement of knowledge of what occurs in evolution at the level of the animals themselves in their intraspecific development. The closer the approach to the animals themselves, rather than to the category, the closer the approach to objectivity in their study.

All three critics agree that perhaps clear cut "insular races" might possibly be full species. One suggests laboratory experiments to establish this. Fertility in the laboratory as a criterion for taxonomic status might lead to some peculiar alignments. Does the "liger" change the specific status of the lion and the tiger? What about the generic standards of *Bison* and *Bos?* To my thinking, students of subspecies in some kinds of mammals, can determine quite accurately whether or not the characters of insular races are of specific or subspecific status. Many workers are inclined to demand intergradation as a criterion for subspecies. In some cases there is no terrain for intergradation, and intergradation would undoubtedly occur if the possibility for it existed. This is the place at which the experience and understanding of the careful, observant student of subspecies, as concerns the amount and kind of genetic fixation, can make a significant contribution to the understanding of the developments of intraspecific evolution. This type of study enables him to evaluate what is happening and what has happened in the gene pool of the population in question. Surely he is interested in the amount and extent of the geographical variation, but of significantly greater importance to him is what makes this variation possible. This variation that he sees is but a window through which the gene pool with its mutations, deletions and additions is visualized. For example, my studies of members of the genus *Thomomys* have enabled me to come to some rather concrete conclusions. I rather doubt that at the level of the subspecies in these animals the small, cumulative mutations and additions to the gene pool have as yet reached sufficient magnitude to be expressed. Studies of many hundreds of specimens of many subspecies of a given species do not reveal any new additions to, or significant changes in,

this pool. In the syngameon of the species are demonstrated all characters to be found in all the subspecies. At the level of subspecies, it appears to be but a reshuffling of the gene pool and the appearance of certain combinations of characters that are already present in the syngameon. When these combinations appear in a frequency that is statistically significant, it indicates that the animals have attained a certain genetic stability—and gene frequency for the distinguishing characters—and they can then be distinguished from other geographic populations. They are then recognized as subspecies. Between species, however, the situation is quite different. At the level of the species, cumulative changes of such magnitude as to cause the obliteration of certain foramina in the skull, the total shifting of positions of foramina, and the different arrangment of bones, must certainly be the result of the expression of the cumulative mutations and therefore constitute new additions to the gene pool. Hence, with this concept of variation, animals from clear-cut insular races are as readily understandable, and can be as easily evaluated taxonomically as those of any other population.

Finally I should like to state that this is not an impassioned appeal to preserve the subspecies. I have attempted to set forth some valid reasons for its preservation. I reiterate that the concept of the subspecies should be preserved, because it is a fine tool for explaining many of the problems of geographic variation, and is of inestimable worth in interpretation. I see no necessity for students who have no need for the subspecies even to enter into its study, but let us retain all tools and make them available to those who possess both the need for them and the skills to use them.

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The Origin of Sexuality

(Concluded from p. 169)

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Points of View

"Degenerate" Coelenterates

The interesting and revolutionary theory of the evolution of Cnidaria proposed by Jovan Hadži necessarily invites discussion and criticism. It is unfortunate that most of the criticism in this country has to be based on only a short presentation of the theory in English, the original not being easily available.

I feel some comment is needed on de Laubenfels' article in a recent issue of this journal (*Syst. Zool., 4*:43–45). Hadži does not base his theory on the fact "that radial symmetry cannot be primitive, that it must be ecologically and secondarily determined." It is true that an extensive knowledge of all groups of invertebrates leads Hadži to the conclusion that radial symmetry is ecologically determined; its evolution is a function of an environment equivalent in all directions of a plane. Sedentary forms usually have such an environment, as do swimming forms under particular conditions of locomotion, e.g. medusae. But the basic contention of the new theory is that life in such an environment *can not form the basis for selection for bilateral symmetry.* Whether or not radial symmetry is a primitive quality is not then germane to this argument.

The "higher" Cnidaria, Anthozoa, show in the arrangement of their septa a general plan of bilateral symmetry which is known to every student of this group. The occurrence of this bilateral arrangement can not be easily explained if it is assumed that this class evolved while sedentary organisms from completely radially symmetrical Scyphozoa or Hydrozoa. If, on the other hand, the evolution proceeded from originally bilateral organisms, then this bilateral arrangement of the septa can be easily interpreted as a remnant of the ancestral organization. De Laubenfels himself gives examples of sedentary organisms which have preserved their original type of symmetry. Their evolution did not continue to the extreme of the radial form, as did the evolution in Echinodermata, or that of tentacular organs in Bryozoa or some sedentary Polychaeta. The use of the Porifera as a proof that sedentary life does not lead to radial symmetry should take into consideration the peculiar colonial structure of these organisms. The very simple Calcispongia are radially symmetrical; this symmetry is lost in colonial forms, giving way not to bilateral symmetry, but to an irregular organization which does not show a preference for any particular direction. Even these forms, when grown in open environment, tend to assume a roughly circular form, often with the main osculum in the center (e.g. Geodea).

The second basic contention of Hadži's theory is that sedentary life frequently results in a simplification of structure, and the author gives many examples to that effect. The uniqueness of "degenerative" evolution is only then apparent. It is well known that parasitic life can produce extreme simplifications of structure and start new evolutionary lines.

In his original work, Hadži gave full consideration to the problem of ontogeny, even though supposing that embryonic development could be so modified that it would not reveal a repetition of phylogeny. He was able to indicate some characteristics of cleavage in Anthozoa which are more reminiscent of Turbellaria than is the case in the other classes of Cnidaria. If the structure of the planula does not support the turbellarian theory (despite its bilateral symmetry) by not showing ancestral organisation—as it should in analogy to the larvae of Cirripedia or Ascidia—it gives also no support to the medusa theory since no stage of the devel-

opment of Anthozoa shows any similarity to medusae. This complete lack of medusoid characters in Anthozoa is considered by Hadži as a primitive character and medusae as an advanced step of evolution within the phylum Cnidaria.

As for the ancestral type of Cnidaria, Hadži suggests an adult form of a rhabdocoelan Turbellarian and not of a planaria-like organism. Neoteny is not a basis for evolutionary theory of Cnidaria, it is a basis for a theory of evolution of Ctenophora which are probably derived from larval forms of Polyclada.

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Editor,
SYSTEMATIC ZOOLOGY:

In my recent paper in SYSTEMATIC ZOOLOGY (*4*:35–40) I discussed briefly (pp. 36–37) the theory that northern populations of the bob-white (*Colinus virginianus*) had been rendered less capable of surviving rigorous winters by hybridization with introduced stock from the southern portion of the species' range. At the time of writing I was unaware that this was any more than a theory, although I believed it to be a reasonable one. I have since learned, with great interest, that this theory has been confirmed experimentally. Since the data were published in a journal likely to be overlooked by systematists and students of evolution, I should like to call the paper to the attention of the readers of SYSTEMATIC ZOOLOGY. It is entitled "The Bobwhite Quail in Pennsylvania," by Roger M. Latham and C. R. Studholme, published as Special Issue No. 4 of *Pennsylvania Game News* in March, 1952. This publication is available from the Pennsylvania Game Commission in Harrisburg.

Comparisons were made among wild-trapped, presumably pure-strain individuals of the northern subspecies from West Virginia and Missouri, and both wild-trapped and pen-reared individuals from Pennsylvania, representing a stock much hybridized with introduced birds from Mexico and the southermost states. It was found that the undiluted strain was clearly superior in its ability to withstand fasting and climatic extremes. The authors correlate their findings with those of Nestler (*Trans. 11th N. A. Wildlife Conf.*, 1946:176–191), who showed that vitamin A is a critical factor in winter survival of bob-whites. Vitamin A is stored in the liver, and it has been demonstrated that liver size diminishes clinally in bob-whites from north to south. I need hardly point out the significance of these discoveries to systematists. We have always assumed that populations within a species are adapted physiologically to their exact environmental conditions, but we have all too few cases in which one of the precise physiological adaptations has so nicely been demonstrated. This case also serves to demonstrate that the immense amount of research now being carried on in the field of wildlife management may well produce certain results of great interest to students of evolution.

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SYSTEMATIC ZOOLOGY is published quarterly by the Society of Systematic Zoology. Its purpose is threefold: To publish, and therefore to encourage the preparation of, contributions on basic aspects of all fields of systematics, principles and problems; to provide a suitable forum for discussion of the problems of the systematist and his methods; and to report as news the other activities of the Society of Systematic Zoology.

Contributions of the following types are solicited: Papers on principles and the applications of principles of wide implication and general interest in any phase of systematics, such as comparative anatomy, zoogeography, paleontology, taxonomy, classification, evolution, or genetics; discussions of methods, specific problems, and activities of systematists; discussions of new books and monographs; and news of systematists, organizations interested in systematics, research and teaching programs, expeditions, collections, meetings, and anything else of interest to systematists.

Consult recent issues for the style to be followed in the preparation of manuscripts. Contributors are encouraged to submit line drawings and diagrams to illustrate their articles. Half-tones may be accepted where necessary to the article.